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Little known Epilamprinae (Dictyoptera: Blaberidae) from the collections of the Muséum d'histoire naturelle de Genève. Part 3

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Abstract: The genus *Morphnodes* Hebard, 1930 is restored from synonymy with *Rhabdoblatta* Kirby, 1903. Detailed morphological descriptions of *Morphna maculata* (Brunner von Wattenwyl, 1865), the type species of the genus *Morphna* Shelford, 1910, of *Morphnodes goliath* (Shelford, 1906), *Pseudocalolampra inexpectata* Roth & Princis, 1971, and *Colapteroblatta compsa* Hebard, 1919, the type species of the genus *Colapteroblatta* Hebard, 1919, are given. The male genitalia of *Morphna maculata* and *Morphnodes goliath* and the ovipositor and adjacent structures of *M. maculata* and *C. compsa* are described for the first time. Relationships of the genera *Morphna*, *Morphnodes* and *Rhabdoblatta* are briefly discussed.

Keywords: Cockroaches - *Morphna maculata* - *Morphnodes goliath* - *Pseudocalolampra inexpectata* - *Colapteroblatta compsa* - morphology.

INTRODUCTION

This paper is devoted to cockroaches of the subfamily Epilamprinae (Blaberidae). It is the third paper of a series of papers dealing with this taxon. The aim of this and previously published papers (Anisyutkin, 2015, 2016) is to provide morphological descriptions which are detailed enough for further phylogenetic investigations.

Morphna maculata (Brunner von Wattenwyl, 1865) and *Colapteroblatta compsa* Hebard, 1919 are the type species of the genera *Morphna* Shelford, 1910 and *Colapteroblatta* Hebard, 1919, respectively. These are the type genera of the tribes Morphnini McKittrick, 1964 and Colapteroblattini Hebard, 1919, respectively. Consequently, the morphology of these species is important for the reconstruction of Epilamprinae phylogeny. The genera *Morphnodes* Hebard, 1930 and *Pseudocalolampra* Roth & Princis, 1971 are insufficiently known and a detailed redescription of their morphology allows us to elucidate their phylogenetic position in the subfamily Epilamprinae.

MATERIAL AND METHODS

This study is mostly based on material deposited in the collection of the Muséum d'histoire naturelle in Geneva. Additional material from the collections of the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia) and of the Natural History Museum of London (United Kingdom) is used as well.

The author generally follows methods described in Anisyutkin (2014, 2015) and Anisyutkin & Yushkova (2017). Rehn's (1951) interpretation of tegmina and wing venation is used. Description of anterior margin of fore femur armament follows Bey-Bienko (1950) and Roth (2003). The terminology of male genital sclerites follows Klass (1997) with some modifications. The terminology used by Grandcolas (1996) for genital structures is given in parentheses. Terminology of female genital structures follows McKittrick (1964) and Klass (1998). Terms introduced by the author (in the present work and in Anisyutkin, 2014, 2015) are given in quotation marks.

Material studied has been deposited in the Muséum d'histoire naturelle in Geneva (MHNG), in the Natural History Museum, London (BMNH) and in the Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg, Russia (ZIN).

Abbreviation used in figures

For further details see text.

a.a. anterior arch of second valvifer of female genitalia;

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a.s.	“additional spines” i.e. spines bordering euplantulae at inside and outside;
a.scl.	“additional sclerite” under basal part of sclerite L2D in male genitalia;
ap.scl.	“apical sclerite” of sclerite L2D in the male genitalia;
ap.t.	“apical tooth” of apical part of sclerite L2D in male genitalia;
b.L2D	basal part of sclerite L2D in male genitalia;
b.L3	basal subsclerite of sclerite L3 in male genitalia;
b.o.	“bent outgrowth” of basal part of sclerite L2D in male genitalia;
bd.s.	brood sac of female genitalia;
bsv.	basivalvula of female genitalia;
c.p.R1T	caudal part of sclerite R1T in male genitalia;
cr.p.R1T	cranial part of sclerite R1T in male genitalia;
d.o.	“dorsal outgrows” of apical part of sclerite L2D in male genitalia;
e.r.	exterior row of spines along lower margin of hind metatarsus;
gg.	gonangulum of female genitalia;
hge.	groove of sclerite L3 in male genitalia (*sensu* Klass, 1997);
i.r.	interior row of spines along lower margin of hind metatarsus;
IX	9th abdominal tergite;
L3, L4U	sclerites in male genitalia;
l.s.	large spines located on lateral sides of metatarsus;
m.a.	membranous area at anteromedian angles of paraprocts;
p.a.	posterolateral angles of abdominal tergite VIII;
par.	paraproct;
pl.	sclerotized lobes of 2nd and 3rd pairs of valves in female genitalia;
r.plm.	right phallomere of male genitalia;
R2, R3, R4, R5	sclerites in male genitalia;
s.t.	“small tooth” of apical part of sclerite L3 in male genitalia;
spi.	spinules located on metatarsal euplantula;
teVIII.	tergal process of 8th abdominal tergite;
teIX.	tergal process of 9th abdominal tergite;
tr.l.	“upper triangular lobe” of right phallomere of male genitalia;
v.I., v.II., v.III.	1st, 2nd and 3rd valves of ovipositor;
vs.	vestibular sclerite in female genitalia;
X	10th abdominal tergite.

TAXONOMIC PART

Genus *Morphna* Shelford, 1910

Type species: *Epilampra maculata* Brunner von Wattenwyl, 1865, by subsequent designation.

Remarks: The genus *Morphna* includes relatively large and wide cockroaches (Figs 1, 3) in comparison with the vast majority of Epilamprinae. The genus is characterized by the structure of its hind tarsi (Figs 14, 15): metatarsus slightly shorter or about as long as other segments combined, with large euplantula along lower margin, tarsal spines few or absent.

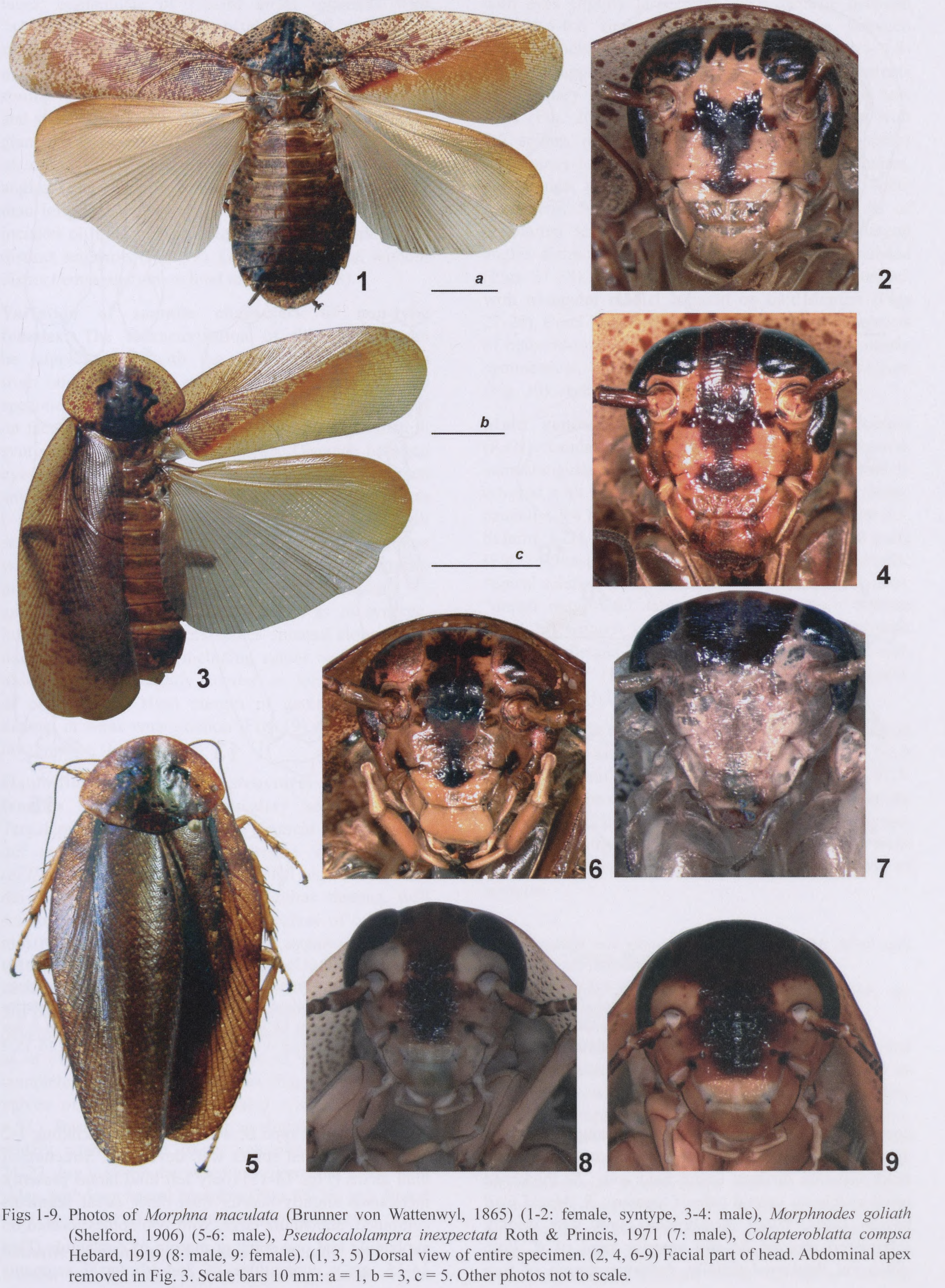
Species included: As given in Beccaloni (2014), with the addition of *M. indica* Anisyutkin in Anisyutkin & Yushkova, 2017 and *M. srilankensis* Anisyutkin in Anisyutkin & Yushkova, 2017.

Morphna maculata (Brunner von Wattenwyl, 1865)

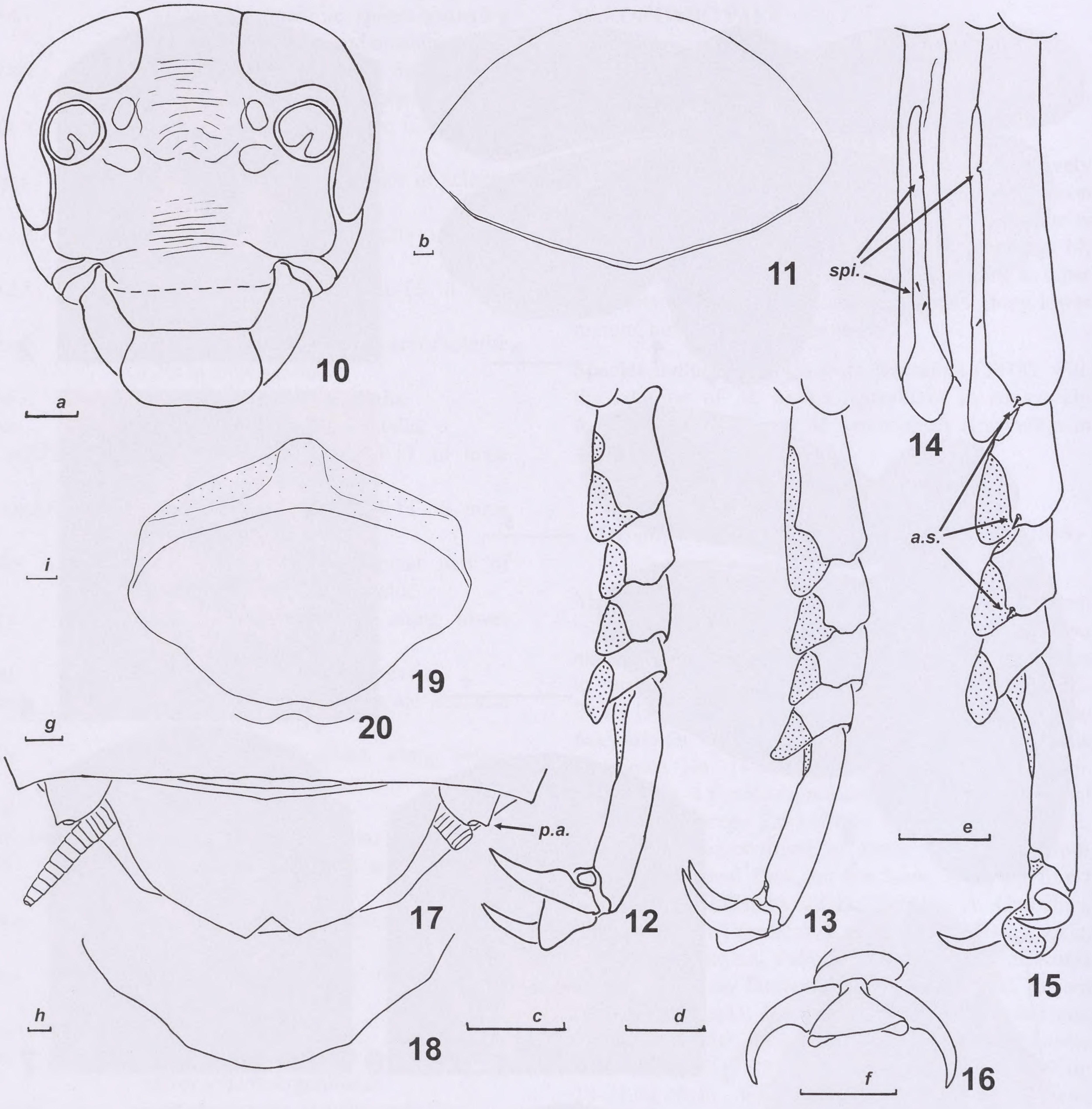
Figs 1-4, 10-43

Material examined: BMNH; female syntype; “Syntype”, “Sarawak. Shelford. 1900-117.”, “*Morphna maculata* Brunner”. – BMNH; 1 male (genital complex in prep. 220317/01); “Malaya Bukit Kutu F.M.S. 28.III.1932, N.C.E. Miller. 1000 ft.”, “*Morphna maculata* Br. W. Det. B. Uvarov 1933”. – ZIN; 1 male (specimen No. 141012/03, genital complex in prep. 220317/02), 1 female (specimen No. 141012/04, genital complex in prep. 220317/03); Malaysia, Borneo I., Sarawak State, environs of Kuching City, environs of Bako National Park, on sea bank, lowlying forest and forest on hills; 18.-22.03.2012; leg. A. Gorochov, M. Berezin, E. Tkatsheva, I. Kamskov. – ZIN; 1 male, 1 female; Malaysia, Pahang State, environs of Kuala Tahan Village on Tembeling River near Taman Negara (= National Park); December 2014; leg. M. Berezin. – ZIN; 1 female; Malaysia, Fraser’s Hill near border with Selangor (17-18 km SW of Raub), 1000-1300 m; 15-23.04.2016; leg. A. Gorochov, M. Berezin, E. Tkatsheva.

Redescription of female syntype (Figs 1-2, 10-18): General colour yellow-brown, with scattered dark dots (Fig. 1). Colouration of head as in Fig. 2, eyes dark brown, facial part of head with arrow-like black spot. Scapi brown, other parts of antennae broken off. Surfaces smooth and lustrous, head with transverse wrinkles (Figs 2, 10), weak punctuation present in proximal part of tegmina, mostly in costal field. Head longer than wide, with indistinct transverse impression between antennal sockets and eyes (Figs 2, 10); ocellar spots small; distance between eyes 0.5 times eye length; distance between antennal sockets about twice scape length (1.5 mm); approximate length ratio of 3rd-5th segments of maxillary palps 0.8 : 1.0 : 1.0. Pronotum as in Figs 1, 11. Tegmina and wings



Figs 1-9. Photos of *Morphna maculata* (Brunner von Wattenwyl, 1865) (1-2: female, syntype, 3-4: male), *Morphnodes goliath* (Shelford, 1906) (5-6: male), *Pseudocalolampra inexpectata* Roth & Princis, 1971 (7: male), *Colapteroblatta compsa* Hebard, 1919 (8: male, 9: female). (1, 3, 5) Dorsal view of entire specimen. (2, 4, 6-9) Facial part of head. Abdominal apex removed in Fig. 3. Scale bars 10 mm: a = 1, b = 3, c = 5. Other photos not to scale.



Figs 10-20. *Morphna maculata* (Brunner von Wattenwyl, 1865), females (10-18: syntype, 19-20: specimen No. 141012/04). (10) Facial part of head. (11) Pronotum, dorsal view. (12-13, 15) Fore (12), mid (13) and hind (15) tarsus, prolateral view. (14) Hind metatarsus, ventral view. (16) Hind pretarsus, distal view. (17) Abdominal apex, dorsal view. (18) Genital plate, outlines of hind margin. (19) Genital plate, ventral view. (20) Genital plate, outline of medial part of hind margin, posterior view. Dotted areas show membranous parts (not shown for metatarsus in Figs 14-15). Abbreviations: *a.s.*, *p.a.*, *spi.* – see paragraph "abbreviation used in figures"; for details see text. Scale bars 1 mm: a = 10, b = 11, c = 12, d = 13, e = 14-15, f = 16, g = 17, h = 18, i = 19-20.

completely developed (Fig. 1), surpassing abdominal apex. Tegmina with truncated apex, sclerotized in costal field; venation distinct; costal field wide; *Sc* thickened (well visible on ventral side of tegmen); *R*, *M* and *CuP* basally fused. Wings membranous, only with weakly sclerotized area of *Sc* and anterior rami of *R*. Fore tibiae not thickened distally. Anterior margin of fore femora of armed type B, with 6-7 spines, including 1-2 apical ones. Tibial spines well developed. Structure of hind tarsus (Figs 14-15) (only left hind tarsus present): metatarsus slightly shorter than other tarsal segments combined, euplantula large, with two spines located on euplantula and one spine at margin of euplantula (Figs 14-15, *spi.*); euplantulae of 2nd-4th tarsal segments

large; euplantulae of 1st-3rd tarsal segments with "additional spines" on their outside (Fig. 15, *a.s.*); claws symmetrical, simple; arolium distinct, about half as long as claw (Fig. 16). Fore (Fig. 12) and mid (Fig. 13) tarsi similar to hind tarsi, but segments comparatively shorter and spines completely absent. Abdomen without visible glandular specializations; spiracle-bearing outgrowths of tergite VIII with sharp and attenuate posterolateral angles (Fig. 17, *p.a.*). Anal plate (tergite X) wider than long and widely rounded, with triangular medial incision on hind margin (Fig. 17). Cerci slender, with distinct segments (Fig. 17). Genital plate wide, without distinct emargination on hind margin (Fig. 18).

Variation of somatic characters of non-type females: The characterization of this species can be supplemented with the following details taken from other specimens examined. Eyes black in some specimens; ocellar spots yellow to orange; black spot on facial part of head in some specimens larger than in syntype. Complete antennae brown. Distance between eyes 0.5-0.6 times eye length; distance between antennal sockets about 1.7-2.0 times scape length (~1.5-1.8 mm); approximate length ratio of 3rd-5th segments of maxillary palps 0.8-1.0 : 1.0 : 1.0. Tegmina with truncated or widely rounded apices. Anterior margin of fore femora with 4-7 spines, including 1-2 apical ones. Structure of hind tarsus as in syntype, but in all other specimens spines situated along lower margin of metatarsus (including spines on euplantula) absent; arolium slightly shorter or longer than half of claw length. Hind margin of genital plate with distinct or weak emargination (Fig. 19) or with sinuate invagination (Fig. 20).

Ovipositor and adjacent structures of non-type females (Figs 21-24): Intercalary sclerite absent. Tergal processes of abdominal segment VIII reduced, not reaching paratergites of tergite VIII (Fig. 21, *teVIII.*); tergal processes of abdominal segment IX fully developed (Fig. 21, *teIX.*). Gonangulum distinct, well sclerotized (Figs 21-23, *gg.*). All valves of ovipositor mostly membranous, only partly sclerotized. First valves large, membranous at apex, with numerous setae along inner side (Fig. 22, *v.I.*). Base of 2nd and 3rd pairs of valves as in Fig. 23, sclerotized lobes well developed (Fig. 23, *pl.*). Anterior arch of second valvifer as in Fig. 23, *a.a.* Second valves of ovipositor small, completely hidden under 1st ones (Fig. 22, *v.II.*). Third valves of ovipositor (gonoplacs) wide (Figs 21-22, *v.III.*). Basivalvula developed as slightly asymmetrical, widely rounded and partly sclerotized plates (Figs 21-23, *bsv.*). Vestibular structure sclerotized along with sides, with long lateral branches (Figs 21-23, *vs.*). Brood sac (Fig. 21, *bd.s.*) without sclerotized structures.

Somatic characters of males: Generally similar to female, but different in the following details. Head with eyes slightly larger (Fig. 25); distance between eyes 0.5-0.6 times eye length; distance between antennal sockets about 1.4-1.5 times scape length (~1.8-1.9 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.0 : 1.0 : 1.1-1.2. Pronotum less wide (Fig. 26). Anterior margin of fore femora with 5-7 spines, including 1-2 apical ones. Tarsal spines (i.e. spines located along lower margin of segments, euplantulae, and "additional spines") absent in some specimens. Shape of spiracle-bearing outgrowths of abdominal tergite VIII quite variable: posterolateral angles distinctly attenuated (Fig. 17, *p.a.*) or rounded (Figs 27-28). Anal plate (tergite X) widely rounded, with triangular medial incision on hind margin (Figs 27-28). Cerci longer (Fig. 27) than in female. Paraprocts of blaberid-type (Figs 28-29, *par.*). Hypandrium nearly symmetrical, hind margin with weak median incision (Fig. 30); styli short, cylindrical.

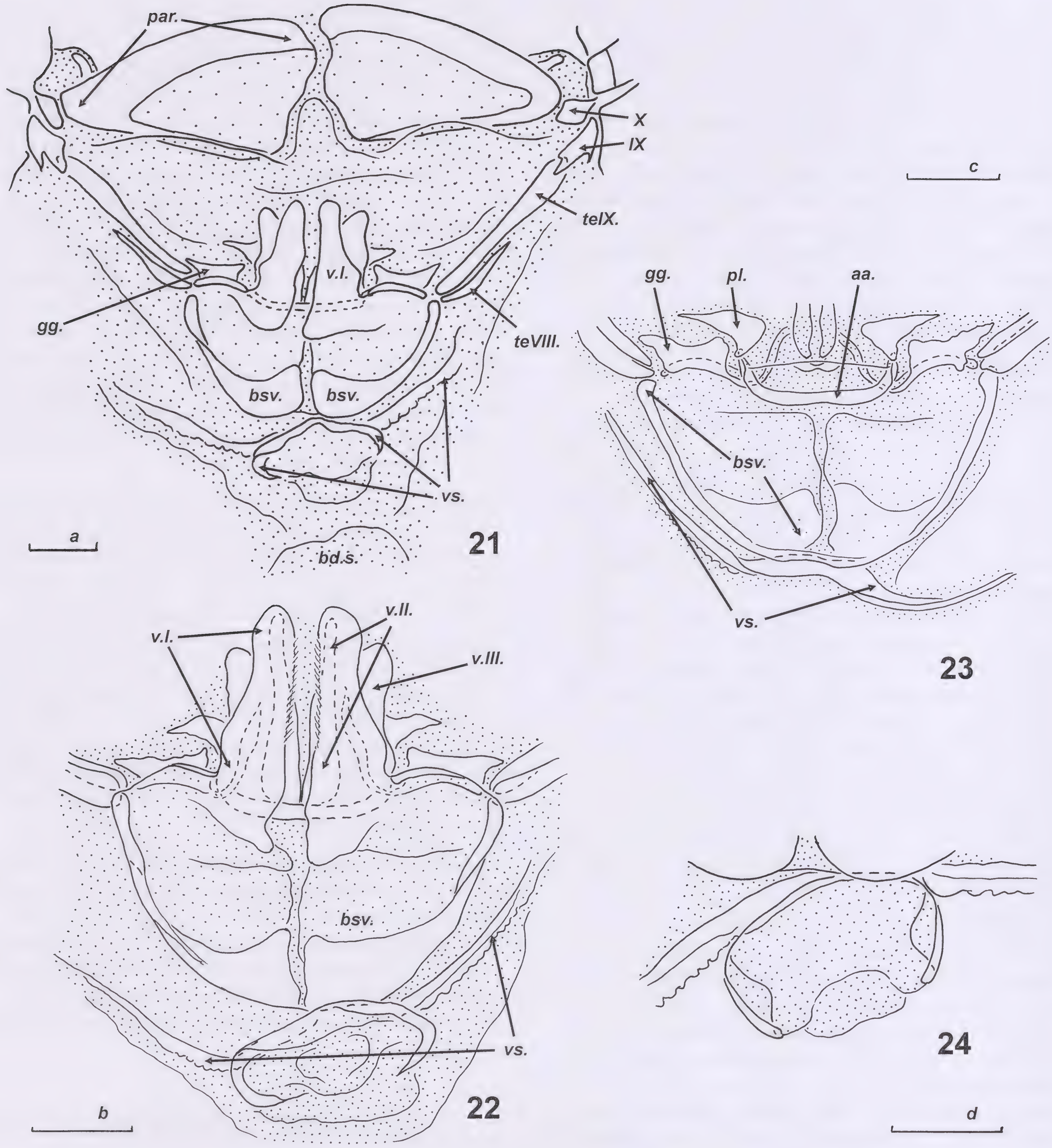
Male genitalia (Figs 31-43): Right phallomere (R+N): caudal part of sclerite R1T well sclerotized, subrectangular in shape (Figs 31-32, *c.p.R1T*), densely covered with bristles; R2 angulate; R3 robust, widened caudally; R4 large, plate-like; R5 small, fused with R3. Sclerite L2D (L1) divided into basal and apical parts (Fig. 33); basal part rod-like, weakly widened cranially; "apical sclerite" partly covered with recumbent bristles; "dorsal outgrowth" large (Figs 34-39, *d.o.*). Sclerite L3 (L2d) without basal subsclerite (Fig. 40); "folded structure" distinct, with short bristles; apex of L3 with "small tooth" (Figs 41-43, *s.t.*); groove *hge* absent. Sclerite L4U (L3d) large.

Dimensions (in mm): Head length: male 6.7-7.2, female 6.7-7.6 (7.1); head width: male 5.8-6.2, female 6.1-6.9 (6.3); pronotum length: male 11.2-11.8, female 11.7-12.4 (11.8); pronotum width: male 16.5-16.7, female 16.5-18.2 (18.2); tegmen length: male 38.0-39.0, female 38.0-40.0 (40.0); tegmen width: male 16.0, female 14.0-17.5 (16.0). Measurements in parenthesis are those of syntype.

Genus *Morphnodes* Hebard, 1930

Type species: *Epilampra vasta* Walker, 1868, by original designation.

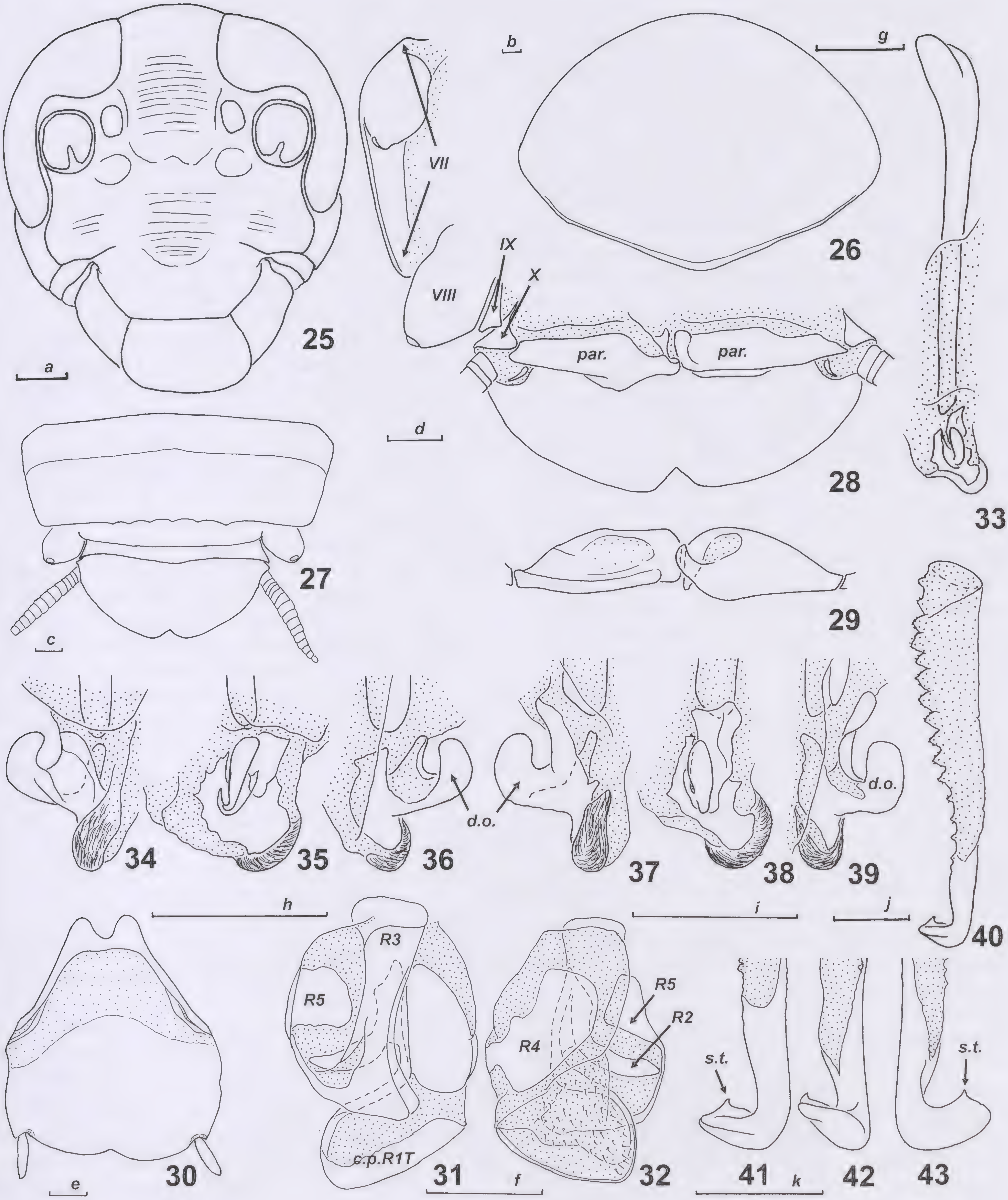
Remarks: The genus *Morphnodes* was described as closely related to *Morphna*, but differs from it as follows: "Pronotal disk with a weak to moderately developed impression latero-cephalad. Tegmina showing distinct distal truncation. Hind metatarsus biseriately spined ventrad." (Hebard, 1930: 93). Later, *Morpnodes* was synonymized with *Pseudophoraspis* Kirby, 1903 by Princis (1958). It was argued that the type species of *Morphnodes*, *E. vasta*, belongs to the genus *Pseudophoraspis* as stated by Shelford (1910). It must be noted that Shelford (1910: 12) did not discuss



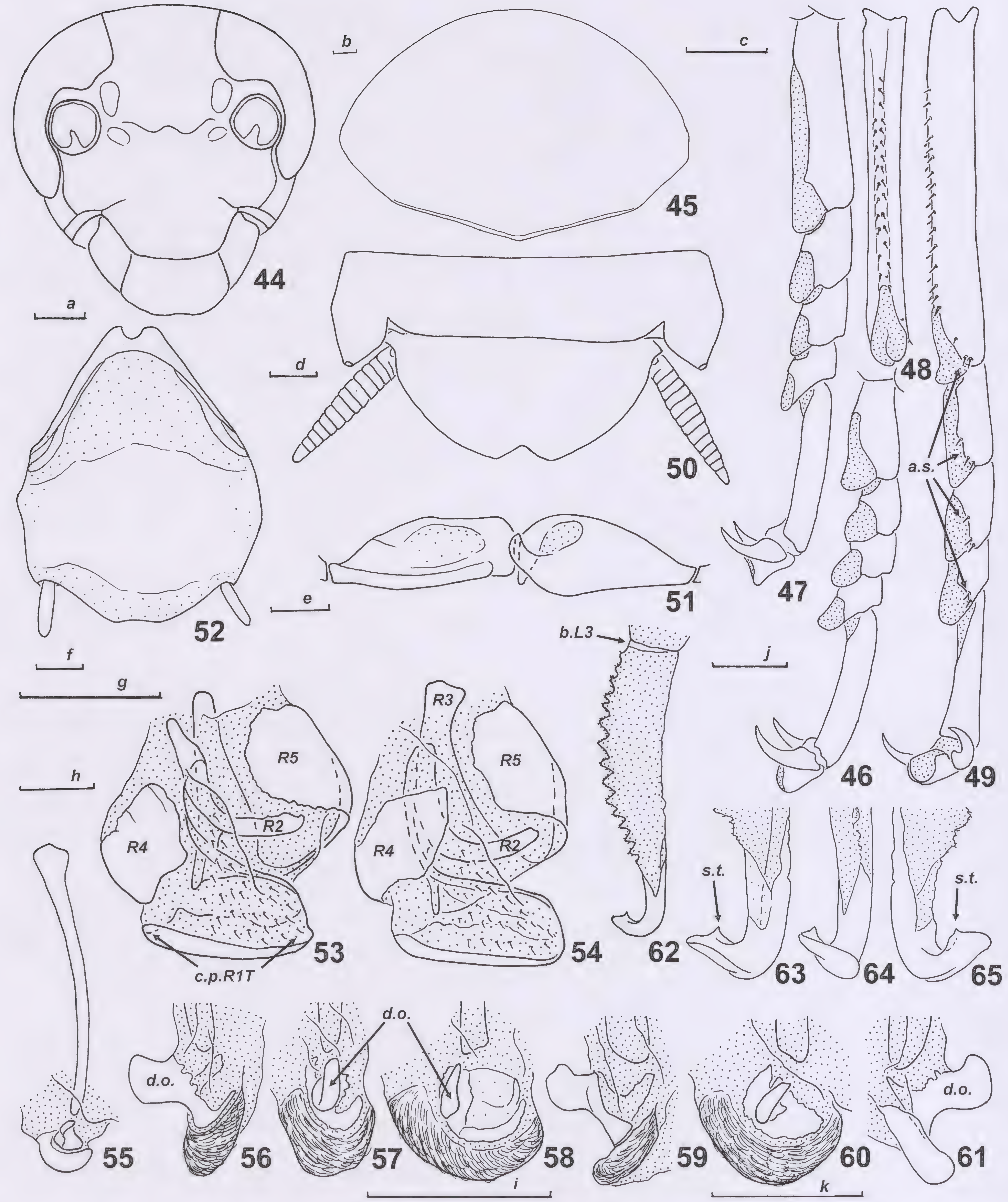
Figs 21-24. *Morphna maculata* (Brunner von Wattenwyl, 1865), female specimen No. 141012/04. (21) Abdominal apex, ventral view, genital plate removed. (22) Ovipositor and adjacent structures, ventral view. (23) Basal part of ovipositor, dorsal view. (24) Vestibular sclerite. Dotted areas show membranous parts, except for valves of ovipositor. Abbreviations: *bd.s.*, *bsv.*, *gg.*, *par.*, *pl.*, *teVIII.*, *teIX.*, *v.I.*, *v.II.*, *v.III.*, *vs.* – see paragraph "abbreviation used in figures"; *IX*, *X* - abdominal tergites IX-X; for details see text. Scale bars 1 mm: a = 21, b = 22, c = 23, d = 24.

the taxonomical position of *E. vasta*, but only listed this species under the genus *Pseudophoraspis*. In 1967 Princis listed *E. vasta* in the genus *Rhabdoblatta* Kirby, 1903 and placed *Morphnodes* in the synonymy of that genus without giving reasons (Princis, 1967).

Morphnodes goliath (Shelford, 1906), redescribed below, is similar to *Morphna maculata*, but differs from this and other representatives of the genus *Morphna* in the structure of the hind tarsi – a character mentioned by Hebard in the original description of the genus *Morphnodes*. *Morphnodes goliath* differs from *Rhabdoblatta praecipua* (Walker, 1868), the type species of the genus



Figs 25-43. *Morphna maculata* (Brunner von Wattenwyl, 1865), males (25-26, 33, 37-43: specimen in BMNH, 27-32, 34-36: specimen in ZIN, No. 141012/03). (25) Facial part of head. (26) Pronotum, dorsal view. (27) Abdominal apex, dorsal view. (28) Abdominal apex, ventral view (only right sides of VII and VIII tergites are shown). (29) Paraprocts, posterior view. (30) Hypandrium, ventral view. (31) Right phallomere, ventral view. (32) Same, dorsal view. (33) Sclerite L2D, dorsal view, bristles not shown. (34, 37) Posterior part of sclerite L2D, lateral view. (35, 38) Same, dorsal view. (36, 39) The same, contralateral view. (40) Sclerite L3. (41-43) Apex of sclerite L3. Dotted areas show membranous parts. Abbreviations: *c.p.R1T*, *d.o.*, *par.*, *R2*, *R3*, *R4*, *R5*, *s.t.* – see paragraph "abbreviation used in figures"; *VII*, *VIII*, *IX*, *X* - abdominal tergites VII-X; for details see text. Scale bars 1 mm: a = 25, b = 26, c = 27, d = 28-29, e = 30, f = 31-32, g = 33, h = 34-36, i = 37-39, j = 40, k = 41-43.



Figs 44-65. *Morphnodes goliath* (Shelford, 1906), specimen in MHNG (44-53, 55, 59-65), specimen No. 200709a (54, 56-57) and specimen No. 200709b (58). (44) Facial part of head. (45) Pronotum, dorsal view. (46-47, 49) Fore (46), mid (47) and hind (49) tarsus, prolateral view. (48) Hind metatarsus, ventral view. (50) Abdominal apex, dorsal view. (51) Paraprocts, ventral view. (52) Hypandrium, ventral view. (53-54) Right phallomere, dorsal view. (55) Sclerite L2D, dorsal view, bristles not shown. (56, 59) Posterior part of sclerite L2D, lateral view. (57-58, 60) Same, dorsal view. (61) Same, contralateral view, bristles not shown. (62) Sclerite L3. (63-65) Apex of sclerite L3. Dotted areas show membranous parts. Abbreviations: *a.s.*, *b.L3*, *c.p.R1T*, *d.o.*, *R2*, *R3*, *R4*, *R5*, *s.t.* see paragraph "abbreviation used in figures"; for details see text. Scale bars 1 mm: a = 44, b = 45, c = 46-49, d = 50, e = 51, f = 52, g = 53-54, h = 55, i = 56-61, j = 62, k = 63-65.

Rhabdoblatta (see redescription in Anisyutkin, 2014), and other species of this genus (Anisyutkin, 2000, 2003) in the presence of a well developed "dorsal outgrowth" of the apical part of sclerite L2D (Figs 56-61) and in the structure of fore and mid tarsi: presence of large euplantulae and absence of any spines (Figs 46-47). In all representatives of *Rhabdoblatta* known to the author all metatarsal euplantulae are small and apical. *Morphnodes goliath* is similar to representatives of the genus *Pseudophoraspis* in the presence of a "dorsal outgrowth" on the apical part of sclerite L2D, but differs from species of *Pseudophoraspis* in the shape of the "dorsal outgrowth". In *M. goliath* the "dorsal outgrowth" is short and directed upward (Figs 56-61, *d.o.*), in contrast to the long and cranial-directed "dorsal outgrowth" of *Pseudophoraspis* species (see Anisyutkin, 1999; Wang *et al.*, 2013). The head structure is also different: in species of *Pseudophoraspis* the facial part of the head has a distinct longitudinal impression (see Anisyutkin, 1999; Wang *et al.*, 2013). The apical part of sclerite L2D in *Pseudophoraspis fruhstorferi* Shelford, 1910 and *P. tramlapensis* Anisyutkin, 1999 have no "dorsal outgrowth" (Anisyutkin, 1999; Wang *et al.*, 2013), but these species probably belong to another genus.

Taking into account the aforementioned, I prefer to restore the genus *Morphnodes* from synonymy. To clarify the status of the genus *Morphnodes*, it is necessary to redescribe the type species, *Epilampra vasta*.

The genera *Morphna* and *Morphnodes* are similar in appearance and in the structure of the male genitalia. They are probably sister-groups with the following synapomorphies: (1) wide costal field of tegmina; (2) fore and mid tarsi with large euplantulae; (3) fore and mid tarsi with reduced spines; (4) "dorsal outgrowth" of apical part of sclerite L2D large and directed upward (large and directed cranially in *Pseudophoraspis*).

A species with a similar venation of the tegmina was described from the Paleocene (Vršanský *et al.*, 2013).

In the catalogues of Princis (1967) and Beccaloni (2014) the date of publication of Hebard's paper is incorrectly given. Volume 81 of the Proceedings of the Academy of Natural Sciences of Philadelphia for the year 1929 was in fact published in 1930, as stated on the first page of the issue.

Included species: *Morphnodes vasta* Walker, 1868, *M. imperatoria* (Stål, 1877), *M. goliath* (Shelford, 1906), *M. miranda* (Shelford, 1906).

Morphnodes goliath (Shelford, 1906)

Figs 5-6, 44-65

Material examined: MHNG; 1 male (genital complex in prep. 240317/01); Malaysia, Sabah State, Mt. Kinabalu, 1550 m; 23.04.1987; leg. C. Besuchet, I. Löbl. – ZIN; 2 males (genital complexes in prep. 240317/02 and 240317/03); Malaysia, Sabah State, Gunung Alab Resort, 1500-1600 m; 25.-28.09.2008; leg. A. Michailov.

Somatic characters of male: General colour brownish, with scattered light dots (Fig. 5). Colouration of head as in Fig. 6, eyes brown or black, facial part of head with large longitudinal dark (brown or black) spot. Scapi and proximal parts of antennae yellowish, distal parts of antennae greyish. Impressions on pronotum blackish. Mouthparts, thorax from below, legs and abdomen yellowish; 3rd-7th abdominal tergites and sternites with pairs of black lateral spots. Surfaces smooth and lustrous, head with several very weak transverse wrinkles between eyes, weak punctuation present in proximal part of tegmina, mostly in costal field. Head slightly longer than wide, with indistinct transverse impression between antennal sockets (Figs 6, 44); ocellar spots small but distinct; distance between eyes 0.6 times eye length; distance between antennal sockets about 1.5-1.6 times scape length (~1.6-1.7 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.0 : 1.0 : 1.2-1.3. Pronotum as in Figs 5, 45, with a pair of impressions; anterior margin widely rounded. Tegmina and wings completely developed (Fig. 5), surpassing abdominal apex. Tegmina with rounded apex, sclerotized in costal field; venation slightly obliterated when seen from above, well visible on ventral side of tegmen; costal field wide; *Sc* thickened (well visible on ventral side of tegmen); *R*, *M* and *CuP* basally fused. Wings membranous, only with weakly sclerotized area of *Sc* and anterior rami of *R*. Fore tibiae not thickened distally. Anterior margin of fore femora of armed type B, with 4-7 spines, including 2 apical ones. Tibial spines well developed. Structure of hind tarsus (Figs 48-49): metatarsus slightly shorter than other tarsal segments combined, with small euplantula and 2 more or less equal rows of spines along lower margin; 2nd-4th segments with large euplantulae, spines along lower margins absent; 1st-3rd segments bordered with 0-3 "additional spines" on inside and outside (Figs 48-49, *a.s.*), in some males "additional spines" absent; claws symmetrical, simple; arolium distinct, about half as long as claw (Fig. 49). Fore (Fig. 46) and mid (Fig. 47) tarsi dissimilar to hind tarsi: metatarsal euplantulae large, spines along lower margin absent; one pair of "additional spines" present only on 1st-3rd segment of mid tarsi of one specimen. Abdomen without visible glandular specializations; spiracle-bearing outgrowths of tergite VIII without attenuate posterolateral angles (Fig. 50). Anal plate (tergite X) with widely rounded hind margin, with a triangular medial incision (Fig. 50). Cerci slender, with distinct segments (Fig. 50). Paraprocts of blaberid-type (Fig. 51). Hypandrium nearly symmetrical, with hind margin between styli projected and membranous, median incision weak (Fig. 52); styli short, cylindrical.

Male genitalia (Figs 53-65): Right phallomere

(R+N): caudal part of sclerite R1T well sclerotized, subrectangular in shape, with more or less attenuate medial angle (Figs 53-54, *c.p.R1T*), densely covered with bristles; R2 angulate; R3 robust, widened caudally; R4 and R5 large, plate-like; R5 fused with R3. Sclerite L2D (L1) divided into basal and apical parts (Fig. 55); basal part rod-like, weakly widened cranially; "apical sclerite" variable in shape (Figs 56-61), covered with recumbent bristles; "dorsal outgrowth" large (Figs 56-61, *d.o.*). Sclerite L3 (L2d) with basal subsclerite (Fig. 62, *b.L3*); "folded structure" distinct, with short bristles; apex of L3 with "small tooth" (Figs 63-65, *s.t.*); groove *hge* absent. Sclerite L4U (L3d) large.

Dimensions (in mm): Head length 5.8-6.0, head width 5.5-5.7; pronotum length 9.1-10.1, pronotum width 13.6-15.1; tegmen length 32.5-45.0, tegmen width 15.0.

Remark: This species was described on the basis of one male from Mt Matang in northern Borneo (Shelford, 1906). The holotype (not examined) is kept in the University Museum of Oxford (Beccaloni, 2014).

Genus *Pseudocalolampra* Roth & Princis, 1971

Type species: *Epilampra pardalina* Walker, 1868, by original designation.

Remarks: This genus was described on the basis of two species from Africa: *P. pardalina* Walker, 1868 (from Kenya to Botswana) and *P. inexpectata* Roth & Princis, 1971 (Kenya). Later, *P. pilosa* Grandcolas, 1993 from Madagascar was added (Grandcolas, 1993).

There are several types of armament along the lower margin of the tarsus. In one of the most common types, two more or less symmetrical rows of spines are present along the lower margin of the tarsus. Each of the two rows of spines (interior and exterior) is situated on a more or less developed longitudinal elevation. These elevations are symmetrical. In my opinion this is a plesiomorphic state, at least for the Blaberidae. In a derived state, one of these elevations is displaced laterally and consequently the corresponding row of spines is displaced to a lateral position (see Anisyutkin, 1999: figs 7-8). This character state is probably a synapomorphy of several genera of Epilamprinae: *Calolamprodes* Bey-Bienko, 1969, *Paracalolamprodes* Anisyutkin, 2015 and *Pseudocalolampra*.

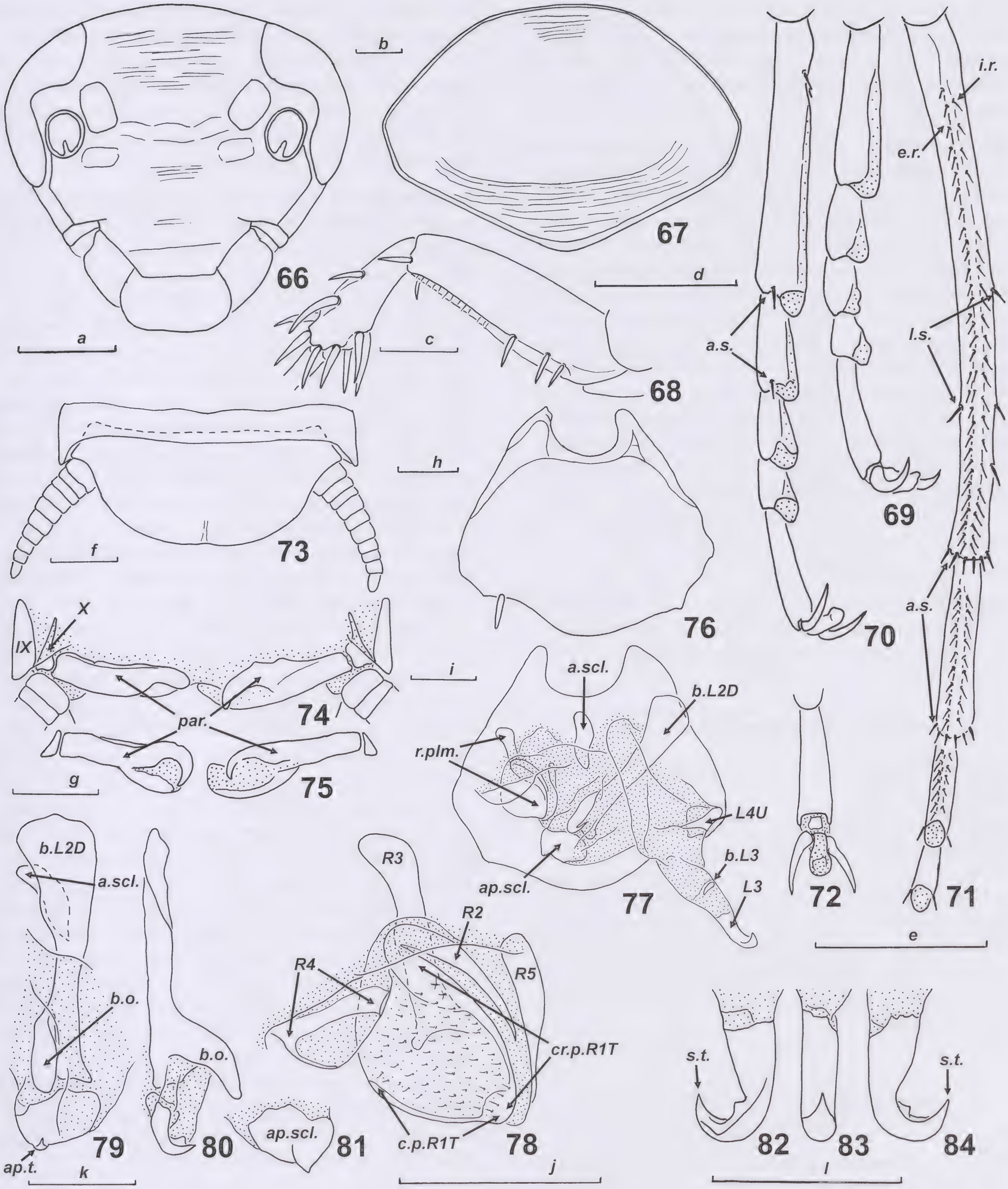
Pseudocalolampra inexpectata Roth & Princis, 1971

Figs 7, 66-84

Material examined: MHNG; 2 males (genital complex of one male in prep. 250317/01); Kenya, Mombasa, Leisure Lodge; 6.-10.06.1980; coll. C. Schomo. – MHNG; 1 male; Kenya, "Leisure L. Jioni Gerch" (handwritten illegible text); 4.06.1981; coll. C. Schomo.

Remarks: The original description (Roth & Princis, 1971) can be supplemented with the following details, based on specimens listed above. The holotype (not examined) of this species is kept in Natural History Museum of London.

Somatic characters of male: General colour yellowish brown, with scattered black dots. Colouration of head as in Fig. 7, eyes black, facial part of head with large black or dark brown spot between eyes. Scapi and about 8-10 proximal segments of antennae yellowish, distal part greyish. Rest of head, mouthparts, legs, thorax and abdomen seen from below dirty yellow. Surfaces smooth and lustrous, head and pronotum with distinct transverse wrinkles (Figs 7, 66-67), weak punctuation present on pronotum. Head wider than long, with large impression between eyes and antennal sockets (Figs 7, 66); ocellar spots large; distance between eyes about as long as eye length; distance between antennal sockets about 2.3-2.7 times scape length (~0.6-0.7 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.1-1.2 : 1.0 : 1.0. Pronotum as in Fig. 67. Tegmina and wings completely developed, surpassing abdominal apex. Tegmina with rounded apex, sclerotized in costal field; venation slightly reticulate; costal field long, about one third of tegmen length, and narrow; *Sc* thickened (well visible on ventral side of tegmen); *R*, *M* and *CuP* basally fused; *CuP* long, about one half of tegmen length. Wings membranous, only with weakly sclerotized area of *Sc* and anterior rami of *R*. Fore tibiae distinctly thickened distally (Fig. 68). Anterior margin of fore femora of armed type B, with 4 spines, including 1 apical one (Fig. 68). Tibial spines well developed. Structure of hind tarsus (Figs 69-72): metatarsus a little longer than other tarsal segments combined, with 2 unequal rows of spines along lower margin: exterior row (Fig. 71, *e.r.*) consisting of 31-37, interior row (Fig. 71, *i.r.*) of 16-23 spines; 2nd and 3rd segments with 10-13/5-8 and 6-9/3-5 spines in exterior and interior rows, respectively; other segments without spines along lower margin; very small euplantulae present on 3rd-4th segments; distal ends of 1st-4th segments bordered with 6, 5 and 3 "additional spines, respectively (Figs 70-71, *a.s.*); 1-3 large spines located on lateral sides of metatarsus (Fig. 71, *l.s.*); interior rows of spines displaced laterally on all segments; claws symmetrical, simple; arolium distinct, about half as long as claw (Figs 69-72). Fore (Fig. 69) and mid (Fig. 70) tarsi dissimilar to hind tarsi: metatarsal euplantulae large, spines along lower margin absent; one pair of "additional spines" present only on 1st-2nd segments of mid tarsi. Abdomen without visible glandular specializations; spiracle-bearing outgrowths of tergite VIII weakly expressed, without attenuate posterolateral angles. Anal plate (tergite X) wider than long, with nearly straight hind margin (Fig. 73). Cerci robust, with distinct segments (Fig. 73). Left and right



Figs 66-84. *Pseudocalolampra inexpectata* Roth & Princis, 1971, male in MHNG. (66) Facial part of head. (67) Pronotum, dorsal view. (68) Right fore leg, prolateral view. (69-70) Fore (69) and mid (70) tarsus, prolateral view. (71) 1st - 4th tarsal segments of right hind tarsus, ventral view. (72) 5th tarsal segment, ventral view. (73) Abdominal apex, dorsal view. (74-75) Paraprocts, ventral (74) and posterior (75) view. (76) Hypandrium, ventral view. (77) Hypandrium and male genitalia, dorsal view. (78) Right phallomere, dorsal view. (79-80) Sclerite L2D, dorsal (79) and lateral (80) view. (81) Apical sclerite L2D, ventral view. (82-84) Apex of sclerite L3. Dotted areas show membranous parts. Abbreviations: *a.s.*, *a.scl.*, *ap.scl.*, *ap.t.*, *b.L2D*, *b.L3*, *b.o.*, *c.p.R1T*, *cr.p.R1T*, *e.r.*, *i.r.*, *l.s.*, *L3*, *L4U*, *par.*, *r.plm.*, *R2*, *R3*, *R4*, *R5*, *s.t.* – see paragraph "abbreviation used in figures"; *IX*, *X* - abdominal tergites IX-X; for details see text. Scale bars 1 mm: a = 66, b = 67, c = 68, d = 69-70, e = 71-72, f = 73, g = 74-75, h = 76, i = 77, j = 78, k = 79-81, l = 82-84.

paraprocts with hook-shaped caudomedial process (Figs 74-75, *par.*). Hypandrium asymmetrical, hind margin between styli projected and rounded (Figs 76-77); right stylus slender and cylindrical, left one vestigial or absent.

Male genitalia (Figs 77-84): Right phallomere (R+N): caudal part of sclerite R1T thin and weakly sclerotized (Fig. 78, *c.p.R1T*), cranial part widely rounded (Fig. 78, *cr.p.R1T*); R1T densely covered with bristles; R2 rounded; R3 long, with cranial part rod-like and caudally forked; R4 only partly sclerotized; R5 elongated. Sclerite L2D (L1) divided into basal and apical parts (Figs 77, 79-80); basal part robust, distinctly widened cranially (Figs 77, 79-80, *b.L2D*), with large "bent outgrowth" at caudal end (Figs 79-80, *b.o.*), "additional sclerite" under basal part of L2D large (Figs 77, 79, *a.scl.*); apical part in shape of flattened, plate-like sclerite (Figs 77, 79-81, *ap.scl.*), with upward-curved "apical tooth" (Figs 79-81, *ap.t.*); bristles absent. Sclerite L3 (L2d) with basal subsclerite (Fig. 77, *b.L3*); "folded structure" and bristles absent; apex of L3 with "small tooth" (Figs 82-84, *s.t.*); groove *hge* absent. Sclerite L4U (L3d) large (Fig. 77).

Dimensions (in mm): Head length 2.8-3.1, head width 3.0-3.2; pronotum length 4.5-5.0, pronotum width 6.5-7.2; tegmen length 17.2-18.0, tegmen width 5.5-6.1.

Genus *Colapteroblatta* Hebard, 1919

Type-species: *Colapteroblatta compsa* Hebard, 1919, by monotypy.

Remarks: The genus was described as monotypical, on the basis of 1 male, 7 females and 3 larvae (Hebard, 1919). The morphology of external structures was described in detail in the original description. The male genitalia of *C. compsa* were illustrated by Roth (1971). Later, the genera *Poroblatta* Hebard, 1919, *Acroporoblatta* Hebard, 1919 and *Nauclidas* Rehn, 1930 were synonymized under *Colapteroblatta* by Roth & Gutiérrez (1998).

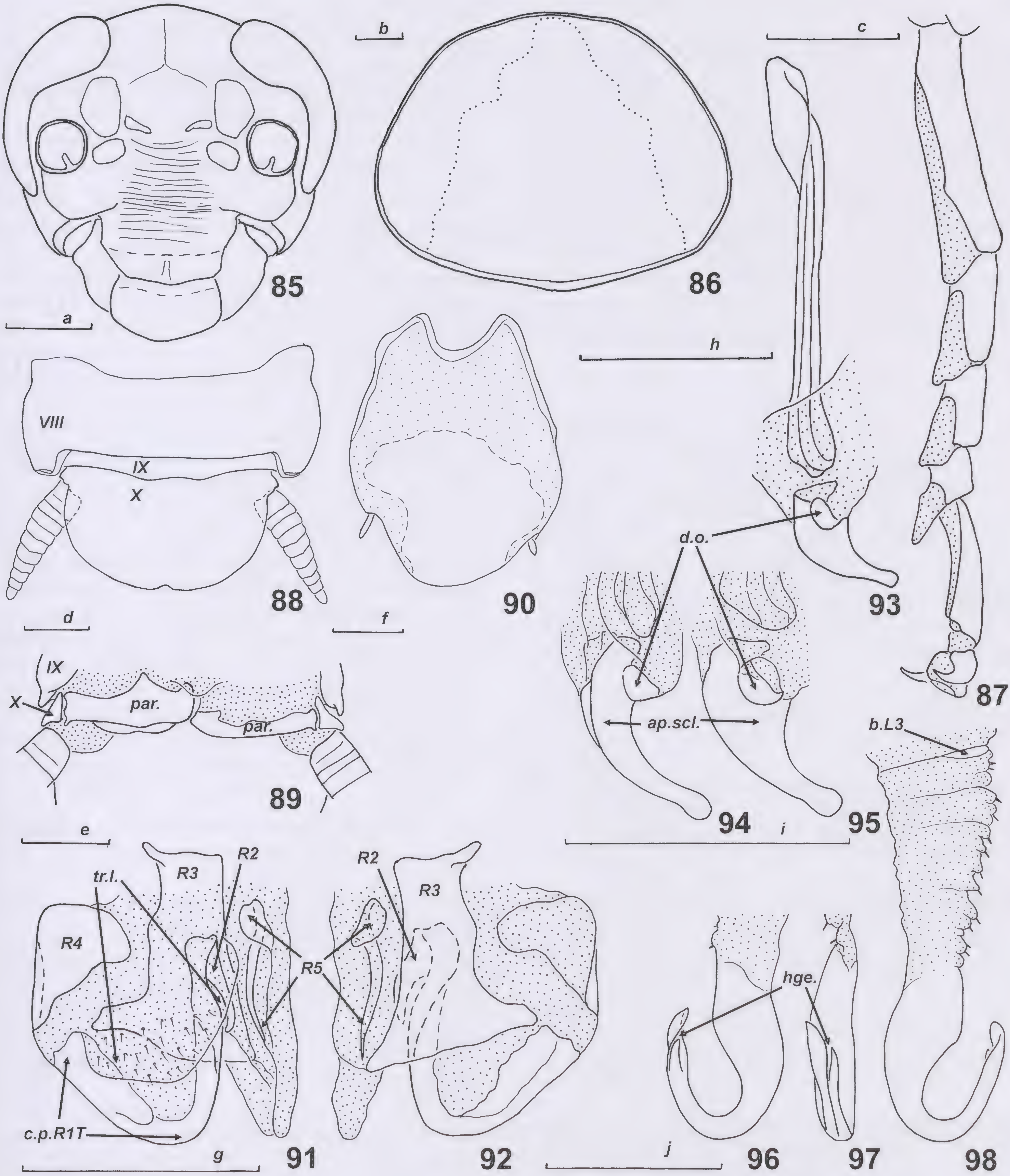
Colapteroblatta compsa Hebard, 1919
Figs 8-9, 85-105

Material examined: MHNG; 1 male; N. Colombia, Dept. Magdalena, N. Sierra Nevada de Sta. Marta, San Lorenzo, 2200 m; 18.-24.08.1985; coll. H.G. Müller, "am Wegrand, aus der Vegetation". – MHHG; 1 female; same data as for the male, but 22.08.1985, "am Wegrand, unter Stein".

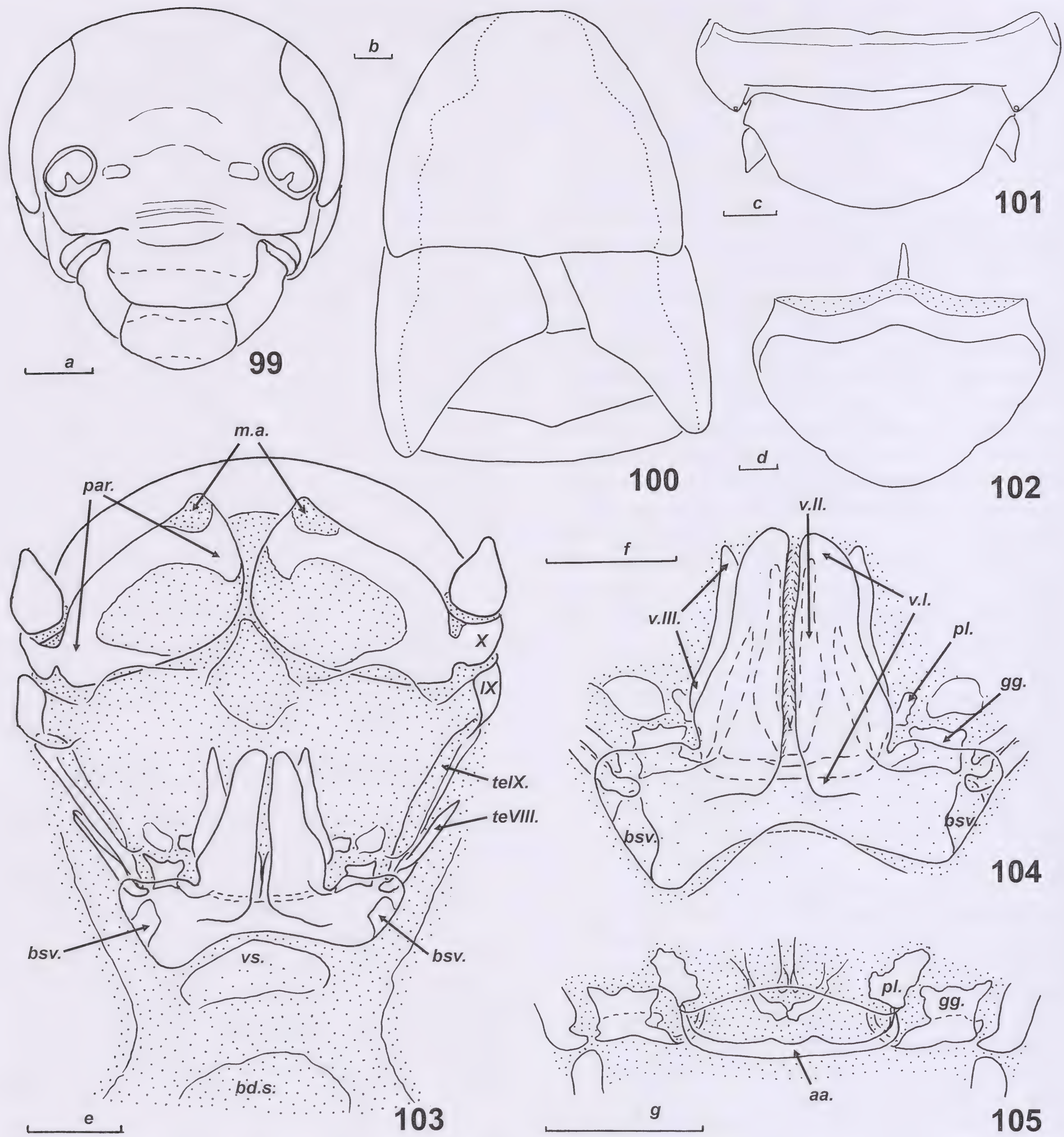
Remarks: The original description (Hebard, 1919) and the data of Roth (1971) and Roth & Gutierrez (1998) are sufficient and a re-examination of the types is therefore not necessary. The type material (not examined) is probably kept in entomological collection of Academy of Natural Sciences of Drexel University (former Academy of Natural Sciences of Philadelphia). The type locality is "San Lorenzo, Sierra Nevada de Santa Maria, Magdalena, Colombia" (Hebard, 1919), i.e. the specimens redescribed below were collected not far away from the type locality. The following supplementary details can be given.

Somatic characters of male: General colour yellowish brown. Colouration of head as in Fig. 8, eyes black, facial part of head with large longitudinal dark brown spot. Antennae yellowish brown. Central part of pronotum dark brown, lateral part yellow (Fig. 86). Surfaces smooth and lustrous; head with transverse wrinkles (Fig. 85); head, pronotum and costal field of tegmina with distinct punctuation. Head longer than wide, vertex projected between eyes, with indistinct transverse impression between antennal sockets (Figs 8, 85); ocellar spots large; distance between eyes 0.8 times eye length; distance between antennal sockets about 0.5 times scape length (~1.2 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.3 : 1.0 : 1.2. Pronotum rounded, with hind margin weakly projected (Fig. 86). Tegmina and wings completely developed, strongly elongated, surpassing abdominal apex. Tegmina membranous, only proximal part of costal field slightly sclerotized; apex rounded; venation distinct; costal field short and narrow; *Sc* thickened (well visible on ventral side of tegmen); *R*, *M* and *CuP* basally fused. Wings membranous. Fore tibiae not thickened distally. Anterior margin of fore femora of armed type C, with single apical spine. Tibial spines well developed. Structure of hind tarsus (Fig. 87): metatarsus distinctly shorter than other tarsal segments combined, with large euplantula; spines absent; claws symmetrical, simple; arolium distinct, about half as long as claw. Fore and mid tarsi similar to hind tarsi but segments comparatively shorter. Abdomen without visible glandular specializations; spiracle-bearing outgrowths of tergite VIII without attenuate posterolateral angles (Fig. 88). Anal plate (tergite X) with widely rounded hind margin with weak medial incision (Fig. 88). Cerci slender, with distinct segments (Fig. 88). Paraprocts of blaberid-type (Fig. 89). Hypandrium asymmetrical, hind margin between styli projected and rounded (Fig. 90); styli short, cylindrical and asymmetrical: right stylus about twice as long as left stylus (Fig. 90).

Male genitalia (Figs 91-98): Right phallomere (R+N): caudal part of sclerite R1T well sclerotized, dorsally with "upper triangular lobe" (Fig. 91, *tr.l.*), this lobe and adjacent membranes covered with bristles; R2 short and nearly straight, slightly rounded in plane perpendicular to plane of figure, not visible in Figs 91-92; R3 robust, widened caudally; R4 large, plate-like; R5 in shape of cranially widened, long and thin strip, surrounded with membranous lobe. Sclerite L2D (L1) divided into basal and apical parts (Fig. 93); basal part rod-like, weakly



Figs 85-98. *Colapteroblatta compsa* Hebard, 1919, male in MHNG. (85) Facial part of head. (86) Pronotum, dorsal view. (87) Hind tarsus, prolateral view. (88) Abdominal apex, dorsal view. (89) Paraprocts, ventral view. (90) Hypandrium, ventral view. (91) Right phallomere, dorsal view. (92) Same, ventral view. (93) Sclerite L2D, dorsal view. (94) Posterior part of sclerite L2D, lateral view. (95) Same, dorsal view. (96-97) Apex of sclerite L3. (98) Sclerite L3. Dotted areas show membranous parts. Dotted line in Fig. 86 delimits yellow lateral stripes and dark central spot. Abbreviations: *ap.scl.*, *b.L3*, *c.p.R1T*, *d.o.*, *hge.*, *par.*, *R2*, *R3*, *R4*, *R5*, *tr.l.* – see paragraph "abbreviation used in figures"; *VIII*, *IX*, *X* - abdominal tergites VIII-X; for details see text. Scale bars 1 mm: a = 85, b = 86, c = 87, d = 88, e = 89, f = 90, g = 91-92, h = 93, i = 94-95, j = 96-98.



Figs. 99-105. *Colapteroblatta compsa* Hebard, 1919, female in MHNG. (99) Facial part of head. (100) Anterior part of body, dorsal view. (101) Abdominal apex, dorsal view. (102) Genital plate, ventral view. (103) Abdominal apex with genital plate removed, ventral view. (104) Ovipositor, ventral view. (105) Basal part of ovipositor, dorsal view. Dotted areas show membranous parts, not indicated on valves of ovipositor. Dotted line in Fig. 100 delimits yellow lateral stripes and dark central part of tergites and tegmina. Abbreviations: *aa.*, *bd.s.*, *bsv.*, *gg.*, *m.a.*, *par.*, *pl.*, *teVIII.*, *teIX.*, *v.I.*, *v.II.*, *v.III.*, *vs.* – see paragraph "abbreviation used in figures"; *IX*, *X* - abdominal tergites IX-X; for details see text. Scale bars 1 mm: a = 99, b = 100, c = 101, d = 102, e = 103, f = 104, g = 105.

widened cranially; apical part in shape of flattened, elongated and plate-like sclerite (Figs 93-95, *ap.scl.*), "dorsal outgrowth" small (Figs 93-95, *d.o.*); bristles absent. Sclerite L3 (L2d) with basal subsclerite (Fig. 98, *b.L3*); "folded structure" distinct, with bristles; apex of L3 attenuated; groove *hge* present (Figs 96-98, *hge.*). Sclerite L4U (L3d) present, weakly sclerotized.

Somatic characters of female: Brachypterous (Fig. 100), body convex, surfaces of abdomen strongly sclerotized. General colour darker than male, blackish; colouration of head as in Fig. 9; pronotum and tegmina with wide lateral yellow strip (Fig. 100); legs dirty yellow. Head with eyes and ocellar spots (Figs 9, 99) smaller than in male; distance between eyes 1.2 times eye length; distance between antennal sockets 2.1 times scape length (~1.1 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.6 : 1.0 : 1.4. Pronotum campaniform, as in Fig. 100. Tegmina strongly abbreviated and malformed, as in Fig. 100; venation absent. Wings vestigial, completely hidden under tegmina. Fore tibiae not thickened distally. Anterior margin of fore femora of armed type C, with 2 apical spines. Tibial spines well developed. Structure of tarsi similar to those of male. Abdomen without visible glandular specializations. Anal plate (tergite X) wider than long, its hind margin widely rounded (Fig. 101). Cerci strongly shortened, conical, with poorly visible traces of segmentation (Fig. 101). Paraprocts medially membranous (Fig. 103, *par.*), fused with anal plate, with membranous area at anteromedian angles (Fig. 103, *m.a.*). Genital plate as in Fig. 102.

Ovipositor and adjacent structures (Figs 103-105): Intercalary sclerite absent. Tergal processes of abdominal segment VIII reduced (Fig. 103, *teVIII.*); tergal processes of abdominal segment IX completely developed (Fig. 103, *teIX.*). Gonangulum distinct, well sclerotized (Figs 103-105, *gg.*). First valves of ovipositor large and membranous (Figs 103-104, *v.I.*), with setae along inner side. Base of 2nd and 3rd pairs of valves as in Fig. 105, sclerotized lobes of irregular shape (Figs 103-105, *pl.*). Anterior arch of second valvifer as in Fig. 105, *a.a.* Second valves of ovipositor small, completely hidden under first ones (Fig. 104, *v.II.*). Third valves of ovipositor (gonoplacs) wide, partly membranous (Figs 103-104, *v.III.*). Basivalvulae in shape of two small and weakly sclerotized plates (Figs 103-104, *bsv.*). Vestibular sclerite weakly sclerotized (Fig. 103, *vs.*). Brood sac (Fig. 103, *bd.s.*) without sclerotized structures.

Dimensions (in mm): Head length: male 3.9, female 5.2; head width: male 3.5, female 4.6; pronotum length: male 5.9, female 7.2; pronotum width: male 7.5, female 7.8; tegmen length: male 44.0, female 5.5; tegmen width: male 7.5, female 5.5.

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REFERENCES

Anisyutkin L.N. 1999. Cockroaches of the subfamily Epilamprinae (Dictyoptera, Blaberidae) from the Indochina Peninsula. *Entomological Review* 79(4): 434-454.

Anisyutkin L.N. 2000. New Cockroach species of the genus *Rhabdoblatta* Kirby (Dictyoptera, Blaberidae) from Southeast Asia: I. *Entomological Review* 80(2): 190-208.

Anisyutkin L.N. 2003. New and little known cockroaches of the genus *Rhabdoblatta* Kirby (Dictyoptera, Blaberidae) from Vietnam and southern China: II. *Entomological Review* 83(5): 540-556.

Anisyutkin L.N. 2014. On cockroaches of the subfamily Epilamprinae (Dictyoptera: Blaberidae) from South India and Sri Lanka, with descriptions of new taxa. *Zootaxa* 3847(3): 301-332.

Anisyutkin L.N. 2015. New and little known known Epilamprinae (Dictyoptera: Blaberidae) from the collections of the Muséum d'histoire naturelle de Genève and the Zoological Institute of Saint Petersburg. Part 1. *Revue suisse de Zoologie* 122(2): 283-296.

Anisyutkin L.N. 2016. New and little known Epilamprinae (Dictyoptera: Blaberidae) from the collections of the Muséum d'histoire naturelle de Genève and the Zoological Institute of Saint Petersburg. Part 2. *Revue suisse de Zoologie* 123(1): 139-152.

Anisyutkin L.N., Yushkova O.V. 2017. New data on cockroaches of the subfamily Epilamprinae (Dictyoptera: Blaberidae) from India and Sri Lanka, with descriptions of new species and the genital complex of *Aptera fusca* (Thunberg, 1784). *Zootaxa* 4236(1): 41-64.

Beccaloni G.W. 2014. Cockroach Species File Online. Version 5.0/5.0. World Wide Web electronic publication. Available at http://Cockroach.SpeciesFile.org (accessed 22 March 2017).

Bey-Bienko G.Y. 1950. Cockroach insects. Fauna USSR, New Series, 40. *Nauka, Moscow and Leningrad*, 343 pp.

Bey-Bienko G.Y. 1969. New genera and species of cockroaches (Blattoptera) from tropical and subtropical Asia. *Entomologicheskoe Obozrenie* 48(4): 831-862.

Brunner von Wattenwyl C. 1865. Nouveau système des Blattaires. *Carl Ueberreuter, Wien*, 426 pp.

Grandcolas P. 1993. Monophylie et structure phylogénétique des [Blaberinae + Zetoborinae + Gyninae + Diplopterinae] (Dictyoptera: Blaberidae). *Annales de la Société entomologique de France (N.S.)* 29(2): 195-222.

Grandcolas P. 1996. The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Canadian Journal of Zoology* 74(3): 508-527.

Hebard M. 1919. Studies in the Dermaptera and Orthoptera of Colombia. *Transactions of the American Entomological Society* 45: 89-179.

Hebard M. 1930. Studies in Malayan Blattidae (Orthoptera). *Proceedings of the Academy of Natural Sciences of Philadelphia* (1929) 81: 1-109.

Kirby W.F. 1903. Notes on Blattidae & c., with description of new genera and species in the collection of the British Museum, South Kensington. No 2. *Annals and Magazine of Natural History* (*Series 7*) 12: 273-280.

Klass K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner Zoologische Monographien* 42: 1-341.

Klass K.-D. 1998. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. *Zoologischer Anzeiger* 236: 69-101.

McKittrick F.A. 1964. Evolutionary studies of cockroaches. *Cornell University Agricultural Experiments Station Memoir* 389: 1-197.

Princis K. 1958. Revision der Walkerschen und Kirbyschen Blattarientypen im British Museum of Natural History, London. II. *Opuscula entomologica* 23: 59-75.

Princis K. 1967. Blattariae: Subordo Epilamproidea. Fam.: Nyctiboridae, Epilampridae. *In*: Beier M. (ed.). *Orthopterorum Catalogus* 11: 615-710.

Rehn J.A.G. 1930. New or little known Neotropical Blattidae (Orthoptera). Number Two. *Transactions of the American Entomological Society* 56: 19-71.

Rehn J.W.H. 1951. Classification of the Blattaria as indicated by their wings (Orthoptera). *Memoirs of the American Entomological Society* 14: 1-134.

Roth L.M. 1971. The male genitalia of Blattaria. VII. *Galiblatta*, *Dryadoblatta*, *Poroblatta*, *Colapteroblatta*, *Nauclidas*, *Notolampra*, *Litopeltis*, and *Cariacasia* (Blaberidae: Epilamprinae). *Psyche* 78: 180-192.

Roth L.M. 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects* 37: 1-186.

Roth L.M., Gutiérrez E. 1998. The cockroach genus *Colapteroblatta*, its synonyms *Poroblatta*, *Acroporoblatta*, and *Nauclidas*, and a new species of *Litopeltis* (Blattaria: Blaberidae, Epilamprinae). *Transactions of the American Entomological Society* 124(3-4): 167-202.

Roth L.M., Princis K. 1971. *Pseudocalolampra*, a new genus of cockroach from Africa. *Proceedings of the Entomological Society of Washington* 73(3): 329-336.

Shelford R. 1906. Studies of the Blattidae. III. Some new Blattidae from Sarawak, Borneo, in the Hope Department, Oxford University Museum. *Transactions of the Entomological Society, London* 1: 265-275.

Shelford R. 1910. Orthoptera. Fam. Blattidae. Subfam. Epilamprinae. *Genera Insectorum* 101: 1-21.

Stål C. 1877. Orthoptera nova ex insulis Philippinis descripsit. Öfversigt ap Kongl. *Vetenskaps-Akademiens Förhandlingar* 10: 33-58.

Vršanský P., Vidlička L., Barna P., Bugdaeva E., Markevich V. 2013. Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia. *Zootaxa* 3635(2): 117-126.

Walker F. 1868. Catalogue of the specimens of Blattariae in the collection of the British Museum. *British Museum, London*, 239 pp.

Wang Z., Wu K., Che Y. 2013. New record of the cockroach genus *Pseudophoraspis* (Blaberidae, Epilamprinae) from China with descriptions of three new species. *ZooKeys* 273: 1-14.

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On the genus *Sunius* Stephens, 1829 of Turkey. V. A new micropterous species from central southern Anatolia, with additional records from the western Mediterranean region (Coleoptera: Staphylinidae: Paederinae)

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Abstract: A new species of the genus *Sunius* Stephens, 1829 is described from the Karaman province of central southern Anatolia: *Sunius tauricus* sp. n. Additional records of seven species and two subspecies of *Sunius* from the western Mediterranean region are reported. A total of 38 species are now known from Turkey, 34 of them are endemic.

Keywords: Coleoptera - Staphylinidae - Paederinae - *Sunius* - Turkey - western Mediterranean - new species.

INTRODUCTION

The genus *Sunius* Stephens, 1829 comprises 136 species in the Palaearctic region, with its main diversity centre in the Mediterranean countries, especially in Anatolia (Assing, 2008a; Anlaş, 2016a, b; Schülke & Smetana, 2015). A total of 37 species are known from Turkey, 33 of which are endemic to that country (Anlaş, 2016b).

In this paper I describe a new species of *Sunius* from central southern Anatolia, rising the diversity of the genus in Turkey to 38 species. Additional records of seven species and two subspecies of *Sunius* from the western Mediterranean region are also reported.

MATERIAL AND METHODS

Terminology of the primary and secondary sexual characters of the species described herein follows Coiffait (1984) and Assing (2008a). The morphological studies were conducted using a Stemi 2000-C microscope (Zeiss Germany). For the photographs a digital camera (Zeiss Axiocam ERC5s) was used.

Head length was measured from the anterior margin of the frons to the posterior margin of the head, length of pronotum was measured along the median line, elytral length was measured at the suture from the apex of the scutellum to the posterior margin of the elytra. The length of the median lobe of the aedeagus was measured from the apex of the ventral process to the base of the capsule.

The material referred to in this study is preserved in the following collections:

AZMM – Alaşehir Zoological Museum, Manisa, Turkey (S. Anlaş).
HNHM – Hungarian Natural History Museum, Budapest, Hungary (G. Makranczy, O. Merkl)
MHNG – Muséum d'Histoire Naturelle, Genève, Switzerland (G. Cuccodoro).

RESULTS

Faunistic Records

Sunius microphthalmus (Franz, 1979)

Material examined: MHNG; 1♂, 1♀; 08.III.1983; Canary Islands, Hierro, El Golfo, 800-1000 m; leg. Besuchet. – MHNG; 1♂; 07.III.1983; Canaries, Hierro, Amoco, 900 m; leg. Besuchet.

Distribution: This species is endemic to the El Hierro Island of the Canary Archipelago (Assing, 2008a).

Sunius brevipennis brevipennis (Wollaston, 1864)

Material examined: MHNG; 1♂, 2♀; 12.III.1983; Canary Islands, Tenerife, Ruigomez, 900 m; leg. Besuchet. – MHNG; 1♂; 14.III.1983; Tenerife, Puerto de la Cruz; leg. Besuchet.

Distribution: This subspecies is endemic to Tenerife in the Canary Islands (Assing, 2008a).

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Sunius brevipennis canariensis (Bernhauer, 1928)

Material examined: MHNG; 3♂, 2♀; 04.III.1983; Canary Islands, Hierro, La Playes; leg. Besuchet.

Distribution: This subspecies occurs only in the Canaries, where it has been found on the islands of Gran Canaria, La Palma, El Hierro and Lanzarote (Assing, 2008a).

Sunius fernandezi Hernández & Garcia, 1982

Material examined: MHNG; 2♂, 1♀; 13.III.1983; Canary Islands, Tenerife, Roque de Caramujo, 2200 m; leg. Besuchet.

Distribution: This species occurs only in the Canaries, where it is restricted to the island of Tenerife (Assing, 2008a).

Sunius ovaliceps (Fauvel, 1878)

Material examined: MHNG; 1♂, 2♀; 10.IX.1969; Portugal, Faro, Aljezur, leg. Senglet. – MHNG; 1♂; XII.1975; Spain, Albacete, Calar del Albumdo, 1400 m; leg. Dehanreng. – MHNG; 1♂, 2♀; 20.V.1960; Spain, Teruel, Noguera, 1550 m; leg. Besuchet. – MHNG; 1♀; 19.V.1960; Spain, Cuenca, Las Torcas; leg. Besuchet.

Distribution: This species is known from France, Spain, Algeria, Morocco, Tunisia, and also the Afrotropical region (Assing, 2008a; Schülke & Smetana, 2015).

Sunius propinquus (Brisout de Barneville, 1867)

Material examined: HNHM; 1♂, 1♀; Italy, Sardinia, Aritzo; leg. Dodero, coll. Fodor. – MHNG; 1♂; 27.VIII.1969; Portugal, Port., Bragança, Moncorvo; leg. Senglet. – MHNG; 1♀; 05.IV.1962; Tunisia, Tunis, Belvidéu; leg. Besuchet.

Distribution: This species is known from Europe in Belgium, France, Italy, Portugal, Spain, and Sweden, and from North Africa in Algeria, Morocco, Madeira Archipelago, and Tunisia (Assing, 2008a; Schülke & Smetana, 2015).

Sunius tronqueti Assing, 2008

Material examined: MHNG; 1♂; 14.V.1960; Spain, Granada, Puerto de la Ragua, 1800 m; leg. Comellini.

Distribution: The recently described species was only known to occur in the Sierra Nevada in Spain (Assing, 2008b).

Sunius algiricus (Coiffait, 1973)

Material examined: HNHM; 2♂; Italy, Sardinia, Lula; leg. A. Dodero, coll. Fodor.

Distribution: This species was known from southern Italy (Calabria and Sicily) in Europe, and from Algeria and Tunisia in North Africa (Assing, 2008a; Schülke & Smetana, 2015). Thus, this species is here reported from Sardinia for the first time.

Sunius sardus Assing, 2008

Material examined: HNHM; 1♂, 2♀; 22.IV.1902, Italy, Sardinia, Campeda; leg. A. Dodero, coll. Fodor.

Distribution: This species occurs only on the Italian island of Sardinia (Assing, 2008a).

TAXONOMY

Sunius tauricus sp. n.
Figs 1-8

Holotype: AZMM; ♂; 28.V.2016; Turkey, Karaman province, Toros Mts., Ayrancı-Erdemli road, Yüğlük Hill, 2180 m, 37°02'49"N 34°00'26"E; leg. Anlaş, Örgel & Yaman.

Paratypes: AZMM, MHNG; 14♂♂, 10♀♀, same data as holotype.

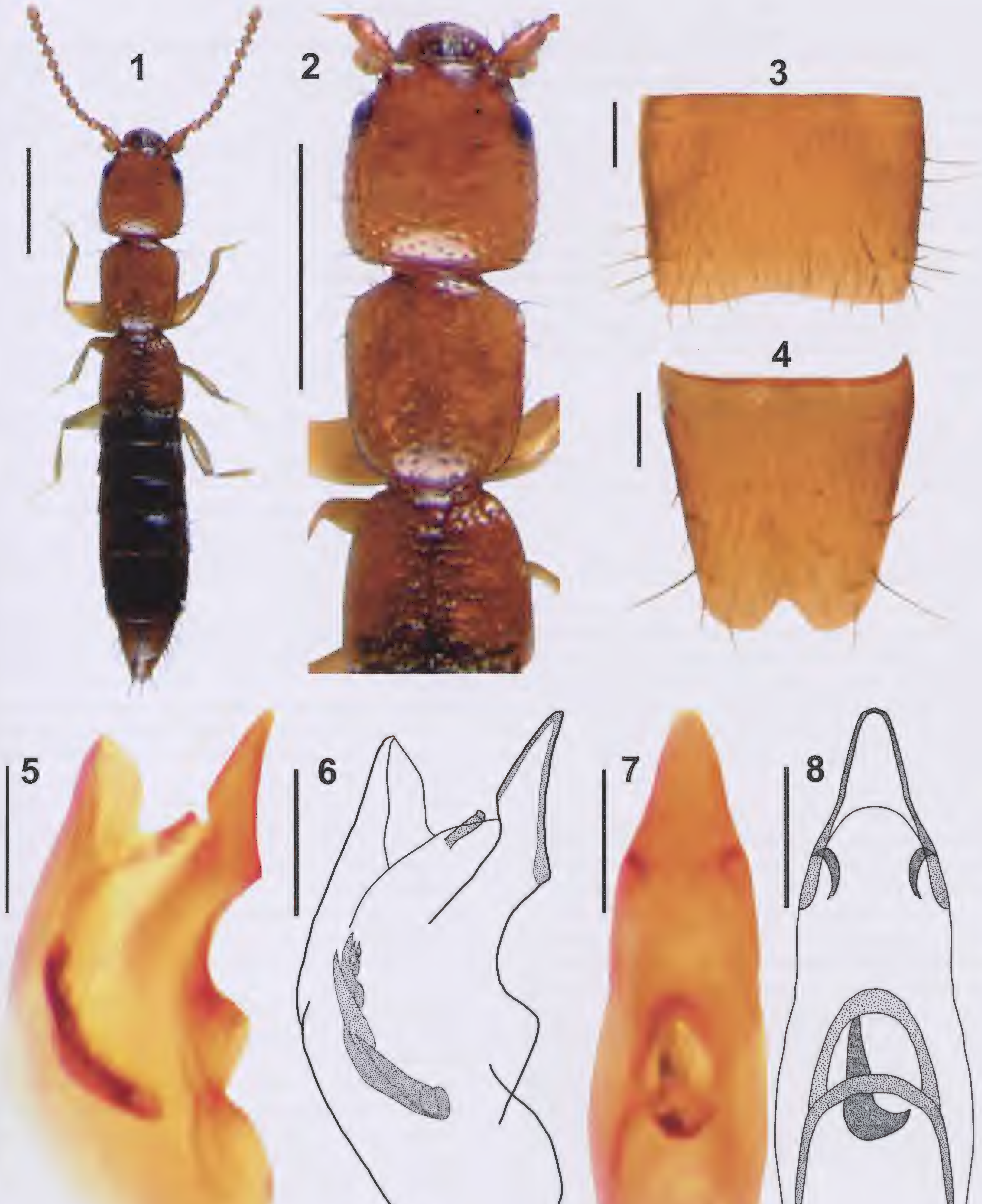
Type locality: Turkey, Karaman Province, Toros Mountain, Yüğlük Hill, 2180 m.

Description: Small species, body length 2.4-2.7 mm. Habitus as in Fig. 1. Colouration: Forebody uniformly reddish; abdomen dark brown; legs pale yellow; antennae reddish.

Head oblong (Figs 1-2), approximately 1.10-1.15 times as long as wide; lateral margins in dorsal view straight and slightly diverging posteriad; punctation coarse, well-defined, and relatively sparse, in lateral area slightly denser than in medio-dorsal area; microsculpture absent, eyes small (Fig. 2), weakly projecting from lateral outline of head, postocular region in dorsal view approximately three times as long as eyes. Antennae moderately slender, approximately 0.80-0.85 mm long.

Pronotum (Fig. 1-2) approximately 0.90-0.95 times as wide as head, and about 1.05-1.10 times as long as wide; lateral margins subparallel and distinctly diverging posteriad in dorsal view; microsculpture absent; punctation as coarse as that of head, medial line impunctate.

Elytra (Figs 1-2) approximately as wide as pronotum and at suture about 0.75 times as long as pronotum; punctation finer and denser than that of pronotum and head, and weakly granulose; microsculpture indistinct. Hind wings strongly reduced.



Figs 1-8. Details of *Sunius tauricus* sp. n. (1) Habitus. (2) Forebody. (3) Male abdominal sternite VII. (4) Male abdominal sternite VIII. (5-6) Aedeagus, lateral view. (7-8) Aedeagus, ventral view. Scale bars: 0.5 mm (1-2); 0.1 mm (3-8).

Abdomen wider than elytra (Fig. 1), approximately 1.05 times as wide as elytra, widest at segments VI-VII; punctation dense and fine; microsculpture shallow; posterior margin of tergite VII without palisade fringe.

Male: Abdominal sternite VII not distinctly modified but posterior margin weakly concave in middle (Fig. 3); posterior margin of sternite VIII with relatively wide emargination, posteriorly with median cluster of very weak pubescence, tubercule absent (Fig. 4); aedeagus approximately 0.35-0.38 mm long, shaped as in Figs 5-8, with apical portion of ventral process slightly dentate in lateral view, base of ventral process in lateral view broadly concave, not deep, and slightly curved, internal sac with a series of six mixed large and small spines.

Distribution and bionomics: The new species was collected only once in the Yüğlük Hill, Taurus Mountains, Karaman province, central southern Anatolia, where it was found under stones at an elevation of 2180 m.

Etymology: The name is derived from the Toros Mountains, the mountain range where the type locality is situated.

Comparative notes: The species is distinguished from all its congeners by the different shape of the ventral process of the aedeagus, and by the shape of the spines of the internal sac. The similarity in the male sexual characters suggests that *S. tauricus* sp. n. is most closely related to *S. tuberiventris* Assing, *S. wunderlei* Assing and *S. balkarensis* Assing (see Assing, 2001). The new species is separated from these species by the lack of tubercule on abdominal sternite VIII (in *S. tuberiventris*: sternite VIII in posterior median area with subcircular tubercle covered with dense pubescence; in *S. wunderlei*: sternite VIII with longer pubescence on posterior median tubercle; in *S. balkarensis*: sternite VIII with slightly smaller tubercle), by the broader and stouter ventral process of the aedeagus in lateral view; by the more shallowly dentate apical portion of the ventral process in lateral view; by the different shape and the series of six spines in the internal sac (in *S. tuberiventris*: internal sac with row of four relatively small spines; in *S. wunderlei*: internal sac with four larger spines; in *S. balkarensis*: internal sac with four larger spines).

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REFERENCES

References of taxon authorities not listed here can be found in Assing (2008a).

Anlaş S. 2016a. On the genus *Sunius* Curtis, 1829 of Turkey III. Four new species from western Anatolia, Turkey (Coleoptera: Staphylinidae: Paederinae). *Zoology in the Middle East* 62(1): 68-77.

Anlaş S. 2016b. On the genus *Sunius* Curtis, 1829 of Turkey. IV. A new micropterous species from southwestern Anatolia and additional records (Coleoptera: Staphylinidae: Paederinae). *Revue suisse de Zoologie* 123(2): 303-306.

Assing V. 2001. On the Turkish species of *Sunius* Curtis 1829 (Coleoptera: Staphylinidae, Paederinae). *Linzer biologische Beiträge* 33: 195-210.

Assing V. 2008a. A revision of the *Sunius* species of the Western Palaearctic region and Middle Asia (Coleoptera: Staphylinidae: Paederinae). *Linzer biologische Beiträge* 40: 5-135.

Assing V. 2008b. Four new species and additional records of Palaearctic *Sunius*, with two new synonymies (Coleoptera: Staphylinidae: Paederinae). *Beiträge zur Entomologie, Keltern*, 58(2): 455-470.

Coiffait H. 1984. Coléoptères staphylinides de la région paléarctique occidentale V. Sous famille Paederinae, Tribu Paederini 2. Sous famille Euaesthetinae. *Nouvelle Revue d'Entomologie, Supplément* 8: 1-424.

Schülke M. & Smetana A. 2015. Staphylinidae, pp. 304-1134. *In:* Löbl I. & Löbl D. (eds), Catalogue of Palaearctic Coleoptera. Volume 2. Hydrophiloidea – Staphylinoidea. Revised and updated edition. *Leiden: Brill:* xxvi + 1702 pp.

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A reassessment of *Halopteris polymorpha* (Billard, 1913) (Cnidaria: Hydrozoa), with descriptions of three new species

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Abstract: Several hydroids, corresponding to various morphotypes included earlier in the synonymy of *Halopteris polymorpha* (Billard, 1913), occur in materials obtained recently from Indonesia and the Maldives, or are housed in the collection of the *Muséum d'histoire naturelle* of Geneva, Switzerland. Among them, new specimens, indistinguishable morphologically from the lectotype, are fully redescribed, together with the so-called variety *sibogae* Billard, 1913. While the latter displays in life an original, not yet documented coloration (bright yellow cauline polyps contrasting with their pure white cladial counterparts), the former is uniformly yellow throughout. This feature, combined with a series of morphological differences, demonstrates that we are dealing with a well-characterized species, whose name should be *H. sibogae* (Billard, 1913). The so far unknown gonothecae of the latter are described for the first time, together with the males of the nominal species. The taxonomy of *H. polymorpha* is analyzed in-depth and reassessed, where available also using 16S DNA sequences. Morphological traits can be used to split the species complex and allow the separation of three as yet undescribed species, *H. australis* from New Caledonia and French Polynesia, *H. millardae* from the Maldives and the Seychelles, and *H. brasiliensis* from Brazil. Additionally, new records of *H. vervoorti* Galea, 2008 extend its known geographical distribution to Madagascar, the Maldives and Indonesia, while some literature records suggest that it could spread as far as Australia, Japan and Fiji. All species are fully described and illustrated, and their morphology is compared to that of their related congeners.

Keywords: Halopterididae - taxonomy - Indo-Pacific - western Atlantic - 16S DNA barcoding.

INTRODUCTION

Hydroids belonging to the Family Halopterididae Millard, 1962 are easily distinguished from other members of the Superfamily Plumularioidea McCrady, 1859 through the presence of cauline hydrothecae (Bouillon *et al.*, 2006). However, according to Schuchert (1997), their identification to species is made occasionally difficult due to the lack of reliable morphological features, or succinct original descriptions, sometimes complicated by the loss of type material.

Among the hydroids collected in the frame of the *Siboga* Expedition, Billard (1913) described a new species, *Halopteris polymorpha*, as well as a variety of it, *H. polymorpha* var. *sibogae*. The latter differs from the nominal species on the account of its long lateral nematothecae, greatly surpassing the hydrothecal rim. Despite this noteworthy difference, it was constantly regarded by many authors (Millard & Bouillon, 1973; Hirohito, 1983, 1995; Schuchert, 1997) as a mere variety, its taxonomic status remaining uncertain until today.

Halopteris polymorpha, as understood by Billard (1913), was based on cormoids originating, sometimes as single specimens, from three different stations of the *Siboga* Expedition, *viz.* Stn. 77, 80 and 299. Other nominal species co-occurred at these localities, namely *H. platygonotheca* Schuchert, 1997 and *H. plagiocampa* (Pictet, 1893) at Stn. 77 (Schuchert, 1997), as well as *H. campanula* (Busk, 1852), *H. nuttingi* (Billard, 1911)

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(Billard, 1913), and *H. diaphragmata* (Billard, 1913) (Schuchert, 1997) at Stn. 80. Among these, Billard (1913) was able to select "*une série de formes*" or, in other words, different morphotypes displaying a panoply of intergrading, though supposedly convergent characters, so as to form his *H. polymorpha*.

Syntype material of *H. polymorpha* was re-examined, redescribed and better illustrated by Schuchert (1997), who also selected as a lectotype the cormoid from *Siboga* Stn. 80. This material is characterized by its notably longer cladial ahydrothecate internodes, shallower hydrothecae, and shorter apophyses supporting the lateral nematothecae, compared to the materials from Stn. 77 and 299. In addition, its hydrocladia are heteromerously segmented, and their ahydrothecate internodes bear commonly two nematothecae. Conversely, in the cormoid from Stn. 77, the hydrocladia are often divided homomerously, and their ahydrothecate internodes are comparatively shorter and bear generally but a single nematotheca. Finally, the cormoid from Stn. 299 is reportedly said to be similar to the lectotype (Billard, 1913; Schuchert, 1997).

Although these morphotypes were pooled together, their morphological and morphometrical features indicate evident differences (Billard, 1913; Schuchert, 1997) that may reflect the involvement of more than one species. However, during over a century, many hydroids with various geographical origins, and exhibiting more or less discrete morphological differences, were included in the synonymy of this taxon, *e.g.* Cape Verde (Ansín Agís *et al.*, 2001), South Africa (Vervoort, 1966; Millard, 1975), Seychelles (Millard & Bouillon, 1973), Indonesia (Di Camillo *et al.*, 2008), Australia (Watson, 2000; Preker & Lawn, 2010, 2012), Coral Sea (Ansín Agís *et al.*, 2009), Fiji (Ryland & Gibbons, 1991), Philippines (Vervoort, 1941, as *Antennella polymorpha*), Guam (Kirkendale & Calder, 2003), and Japan (Hirohito, 1983).

In addition, a series of records of hydroids assigned to *H. buskii* (Bale, 1884) were also included in the synonymy of *H. polymorpha* (see Schuchert, 1997; Ansín Agís *et al.*, 2009), *viz.* Zanzibar (Rees & Vervoort, 1987), India (Thornely, 1916), Sri Lanka (Thornely, 1904), Christmas I. (Ritchie, 1910), Australia (Preker, 2001, 2005), New Caledonia (Redier, 1966), Fiji (Ryland & Gibbons, 1991), French Polynesia (Vervoort & Vasseur, 1977), Philippines (Nutting, 1927), Japan (Hirohito, 1974, 1983, 1995), Hawai'i (Hartlaub, 1901), and Brazil (Migotto, 1996).

Rare, further assignations, such as *Antennella secundaria* (Gmelin, 1791) (Vervoort, 1967, Red Sea) and *Plumularia nuttingi* Billard, 1911 (original account, Indonesia), were also considered as belonging to *H. polymorpha* [Ansín Agís *et al.* (2009) and Schuchert (1997), respectively].

Recent surveys of the hydrozoan fauna of Bali, Ambon and Siladen in Indonesia, and of the Faafu Atoll in the Republic of Maldives, revealed the presence of a number of morphotypes dealt with in some of the literature records mentioned above. Some others (originating from Madagascar, the Seychelles, New Caledonia, and Brazil) are housed in the collection of *Muséum d'histoire naturelle* of Geneva, Switzerland, and were examined for the purpose of the present study, with the aim of reassessing their morphological characters in order to establish their true relationships.

Since DNA extracts could only be obtained for a subset of the described species (Appendix 2), a genetic study was not intended as the primary goal of the present work. However, even if partly incomplete, the available 16S data represent nevertheless crucial, independent evidence for the validity of the concerned taxa and their relationship to other congeners.

MATERIAL AND METHODS

Sampling was done by scuba diving (0-50 m) or snorkeling (0-1 m). Hydroid colonies were carefully removed from their substrate using haemostatic forceps so as to preserve the integrity of the adjacent fauna. The collected specimens were fixed in 4% borax-buffered formalin in seawater and, sometimes, in 90% ethanol for molecular studies. Although the coloration was documented in living material, most observations were done on formalin-preserved specimens, using the methods described in Galea (2007, 2008). Representative samples were deposited in collections of *Muséum d'histoire naturelle* of Geneva, Switzerland, and registration codes are indicated by MHNG-INVE- followed by five-digit numbers. Additional samples dealt with herein are housed in the Naturalis Biodiversity Center (NBC), Leiden, The Netherlands, the *Muséum national d'Histoire naturelle*, Paris, France (MNHN), the *Musée Royal de l'Afrique Centrale*, Tervuren, Belgium (MRAC), as well as in the private collections of the authors (the registration codes are indicated by HRG-, CDC-, and DM&SM-, respectively, followed by numbers, or combinations of letters and numbers).

Genomic DNA was extracted from ethanol-fixed samples following either the protocols described in Zietara *et al.* (2000) or Coffroth *et al.* (1992). A fragment of the *16S rRNA* gene was amplified using hydrozoan-specific primers and protocol described in Cunningham & Buss (1993). PCR products were purified and then sequenced using an ABI 3730xl DNA Analyzer (Applied Biosystem, CA, USA). Sequences were examined manually from chromatogram files using Sequencher v. 4.1.4 (Gene Codes Corporation) and were submitted to the NCBI GenBank database (for accession numbers see Appendix 2). Sequences from this study were aligned with sequences downloaded from GenBank belonging to other representatives of Halopterididae and outgroups using the EINS-i option of MAFFT v. 7.110 (Katoh & Standley, 2013). Sequence alignments were run through Gblocks (Castresana, 2000) using the default 'less

stringent' settings. jModelTest v.2 (Darriba *et al.*, 2012) was used to determine the best-fitting molecular model (Akaike information criterion: GTR+I+Γ). Phylogenetic analyses were performed using RAxML v. 8.2.10 (Stamatakis, 2014) and MrBayes v. 3.2 (Ronquist *et al.*, 2012) for maximum likelihood (ML) and Bayesian inference (BI) analyses, respectively. For the maximum likelihood analysis, clade stability was assessed by bootstrap analysis (1000 replicates) and for the Bayesian analysis, four parallel MCMC runs were run for 5×10^6 generations, sampling every 100 steps, and burn-in was set to 25%.

In addition to the material described in the next section, specimens of the following *Halopteris* species were examined and compared. See also Appendices 1 and 2 for more examined material and data.

H. alternata (Nutting, 1900):
HRG-0890; France, Martinique, Sainte Anne, 14.44095° -60.89626, 10-15 m, coll. H.R. Galea; 11.02.2012; several stems, up to 2.3 cm high, mostly fertile and bearing gonothecae of both sexes. – HRG-1341; France, Martinique, Case-Pilote, 14.64337° -61.14199°, 1-2.5 m, coll. R. Ferry; 24.07.2017; several sterile cormoids, 0.5-1.6 cm high; 16S sequence MF773748.

H. concava (Billard, 1911):
HRG-0990; Indonesia, Tukangbesi Archipelago, Hoga I., -5.44633° 123.76417°, 20 m, coll. G. Allard; 27.09.2011; a few fragmented stems, up to 2.5 cm high, some cladia bearing female gonothecae.

H. liechtensternii (Marktanner-Turneretscher, 1890):
HRG-0120; France, La Ciotat, Mugel creek, 43.16404° 5.60770°, 0.5 m, coll. H.R. Galea; 20.08.2002; numerous plumes, up to 2.5 cm high, some bearing female gonothecae. – HRG-0162; France, La Ciotat, Mugel creek, 43.16404° 5.60770°, 1 m, coll. H.R. Galea; 13.08.2009; numerous plumes, up to 2.6 cm high, with gonothecae of both sexes present.

H. platygonotheca Schuchert, 1997:
MHNG-INVE-97928; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.274168° 115.59264°, 22 m, coll. H.R. Galea; 29.09.2016; 6 cormoids, 25-35 mm high, of which 5 bear female gonothecae; 16S sequence MF784527. – MHNG-INVE-97943; Indonesia, Bali, Tulamben, Drop-off, -8.27841° 115.59599°, 10-15 m, coll. H.R. Galea; 31.01.2017; 7 cormoids, 13-34 mm high, of which 2 are fertile and bear gonothecae of both sexes. – MHNG-INVE-97944; Indonesia, Bali, Tulamben, Drop-off, -8.27841° 115.59599°, 10-15 m, coll. H.R. Galea; 31.01.2017; 19 cormoids, 17-35 mm high, nearly all fertile, bearing either male or female gonothecae, or both; 16S sequence MF784532. – MHNG-INVE-97935; Indonesia, Bali, Banyuning, Japanese shipwreck, -8.3560° 115.6925°, 0-20 m, coll. H.R. Galea; 04.10.2016; one 1.5 cm high cormoid in alcohol, one cormoid on microslide (after DNA extraction); 16S sequence MF784529. – DM&SM-MA0416141; Republic of Maldives, Faafu Atoll, 3.09008° 72.96792°, 12 m, coll. D. Maggioni & S. Montano; 18.04.2016; 5 sterile stems, 6-11 mm high; 16S sequence MF773744. – DM&SM-MA0416149; Republic of Maldives, Faafu Atoll, 3.09383° 72.96650°, 13 m, coll. D. Maggioni & S. Montano; 18.04.2016; 5 sterile stems, 7-13 mm high; 16S sequence MF773745. – DM&SM-MA0416168; Republic of Maldives, Faafu Atoll, 3.09008° 72.96792°, 20 m, coll. D. Maggioni & S. Montano; 20.04.2016; 5 sterile stems, 4-16 mm high; 16S sequence MF773746.

H. tenella (Verrill, 1874):
HRG-0893; France, Martinique, Le Prêcheur, Pointe Lamare, 14.780460° -61.21193°, 10-17 m, coll. H.R. Galea; 14.02.2012; two colonies with stems up to 0.9 cm high, many bearing male gonothecae. – HRG-0894; France, Martinique, Le Prêcheur, Pointe Lamare, 14.780460° -61.21193°, 4-10 m, coll. H.R. Galea; 28.01.2012; a colony with stems up to 0.7 cm high, some bearing female gonothecae.

TAXONOMY AND RESULTS

Order Leptothecata Cornelius, 1992
Family Halopterididae Millard, 1962
Genus *Halopteris* Allman, 1888

Halopteris polymorpha (Billard, 1913)

Figs 1A, 2A, 3A-K; Tables 1, 2; Appendix 1

Plumularia polymorpha Billard, 1913 (*pro parte*): 24, figs 14A, 15. – Van Soest, 1976: 89.

non *Plumularia polymorpha* Billard, 1913 (*pro parte*): 24, fig. 14B, C.

Thecocarpus polymorphus – Bedot, 1921: 9. – Von Schenck, 1965: 928.

Heterotheca polymorpha – Stechow, 1923: 15.

Halopteris polymorpha – (?) Pennycuik, 1959: 178. – Schuchert, 1997 (*pro parte*): 64, fig. 20A, C-F. – Ryland & Gibbons, 1991: 530, fig. 4. – Di Camillo *et al.*, 2008: 1592.

non *Halopteris polymorpha* – Vervoort, 1966: 132, fig. 35. – Millard & Bouillon (*pro parte*), 1973: 83, fig. 10F-H, J; 1974: 9. – Millard, 1975: 354, fig. 112G-L; 1977: 107; 1978: 193; 1980: 132. – Hirohito, 1983: 62, fig. 31. – Bouillon *et al.*, 1995: 49. – Schuchert, 1997 (*pro parte*): 64, figs 20B, 21-23. – Watson, 2000: 46, fig. 35. – Ansín Agís *et al.*, 2001: 167, fig. 70. – Preker, 2001: 154. – Kirkendale & Calder, 2003: 169. – Preker, 2005: 49. – Preker & Lawn, 2005: 342. – Ansín Agís *et al.*, 2009: 53. – Preker & Lawn, 2010: 120; 2012: 45, fig. 7.

non *Antennella polymorpha* – Vervoort, 1941: 218.

non *Antennella secundaria* – Vervoort, 1967: 42, fig. 12 [not *Antennella secundaria* (Gmelin, 1791)].

non *Plumularia nuttingi* Billard, 1911: 66, fig. 8 – Van Soest, 1976: 89.

non *Plumularia buskii* – Thornely, 1904: 120. – Ritchie, 1910: 832. – Thornely, 1916: 150. – Nutting, 1927: 221.

non *Plumularia buski* – Hartlaub, 1901: 374, pl. 22 figs 22, 32, 36. – Billard, 1913: 21, fig. 11, pl. 1 fig. 15. – Redier, 1966: 90, pl. 2 figs 1 & 3, pl. 3 fig. 1 (incorrect subsequent spelling).

non *Heterotheca buski* – Hirohito, 1974: 30, fig. 14 (incorrect subsequent spelling).

non *Halopteris buskii* – Vervoort & Vasseur, 1977: 72, fig. 31. – Rees & Vervoort, 1987 (*pro parte*): 119, fig. 25A-B. – Ryland & Gibbons, 1991: 527, fig. 2. – Bouillon *et al.*, 1995: 49. – Migotto, 1996: 48, fig. 9F-H. – Preker, 2001: 154; 2005: 48.

non *Halopteris buski* – Rees & Thursfield, 1965: 160. – Hirohito, 1983: 61; 1995: 244, fig. 82 (incorrect subsequent spelling).

Material examined: MHNG-INVE-97937; Indonesia, Bali, Padangbai, Jepun shipwreck, -8.52819° 115.51478°, 20 m, coll. H. R. Galea; 06.10.2016; several sterile plumes, up to 3.7 cm high; 16S sequence MF784530. – MNHG-INVE-97951; Indonesia, Bunaken National Marine Park, Manado Tua I., Negeri, 1.61684° 124.70140°, 10 m, coll. G. Allard; 22.11.2010; several plumes, up to 3.7 cm high, some bearing female gonothecae. – HRG-0421; Indonesia, Bunaken National Marine Park, off Bunaken I., Leukan 2, 1.59989° 124.76697°, 10 m, coll. G. Allard; 21.11.2010; 6 stems up to 3 cm high, one of which bears female gonothecae, and three others carrying male gonothecae. – CDC002; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.27417° 115.59265°, 18 m, coll. C. G. Di Camillo; 21.10.2008; two sterile cormoids, 14 and 21 mm high. – CDC003; Indonesia, Ambon, Laha I., -3.69221° 128.12310°, 10-15 m, coll. C. G. Di Camillo; 14.10.2008; a 17 mm high cormoid and a 12 mm high fragment, both infertile. – CDC004; Indonesia, Bunaken National Marine Park, Raymond's Point, 1.62713° 124.73363°, 40-50 m, coll. C. G. Di Camillo; 01.09.2003; two sterile fragments, 7 and 16 mm high, likely from different cormoids. – CDC005; Indonesia, Bunaken National Marine Park, Mandolin's Point, 1.61095° 124.73257°, 20 m, coll. C. G. Di Camillo; 12.02.2005; a 27 mm high cormoid bearing a gonotheca, probably male.

Additional material: MNHN H.L.1309; Indonesia, Rote Island, Buka Bay, -10.87333 123.01833, 34 m, *Siboga* Stn. 299; a 1.1 cm high sterile cormoid belonging to the syntype of *Plumularia polymorpha* Billard, 1913.

Diagnosis: *Halopteris* with cormoids reaching heights of up to 3.7 cm, with monosiphonic, unbranched stems, divided homomerously into rather long internodes bearing a hydrotheca, a lateral apophysis, and up to 9 nematothecae [1 mesial, a pair of laterals, an axillar one, and generally 2-3 (though up to 5 possibly present) above hydrotheca]. Cladia alternately arranged along stem, heteromerously divided into internodes; hydrothecate internodes slightly shorter than their ahydrothecate counterparts, carrying a hydrotheca and its up to 4 associated nematothecae (1 mesial, a pair of laterals, and occasionally an axillar one); ahydrothecate internodes with 1-2 nematothecae. Hydrothecae conical and shallow; lateral nematothecae with either lowered, emarginated or sinuated margin adaxially, not surpassing hydrothecal rim, borne on inconspicuous apophyses. Female gonotheca broadly ovoid, with apical, large, rounded aperture perpendicular to long axis of the theca, and closed by glass-watch-shaped operculum; 2-3 basal nematothecae. Male gonotheca smaller than female, ovoid, without noticeable aperture, with 2 basal nematothecae. Cormoids yellow throughout in life.

Description: Colonies composed of a varied number of cormoids arising from creeping, branching stolon, not carrying nematothecae. Cormoids erect (though flaccid when out of liquid), up to 3.7 cm high. Cauli simple, monosiphonic (Figs 1A, 2A), composed of an up to 1 cm long, ahydrothecate, proximal part above origin from stolon, and a much longer, distal part carrying both hydrothecae and hydrocladia. Basal part usually divided by up to 4 transverse nodes into segments of varied length, bearing a number of nematothecae (up to 34 observed) arranged into two parallel, closely-set rows; distalmost segment delimited from the remainder of caulus through a deeply-cut, oblique node. Stem above basal part longer, homomerously segmented into up to 37 internodes trough oblique constrictions of the perisarc (Fig. 3A); internodes long, bearing one hydrotheca in their lower third, a number of nematothecae, and an apophysis lateral to the hydrotheca supporting a cladium (two apophyses are usually present in the proximal most internode, and these support a pair of cladia) (Fig. 3B); nematothecae: one mesial, a pair of laterals, one axillar, as well as usually 2-3 (though occasionally 1-5 possibly present) above the hydrotheca, arranged in two closely-set rows. Cladia, except for the proximal most that can be paired, alternately-arranged along caulus; up to 5 mm long, usually less so; each composed of a short, proximal, athecate, quadrangular segment, followed by a succession of ahydrothecate and hydrothecate internodes, delimited through a heteromerous segmentation; ahydrothecate internodes with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes. First ahydrothecate internode quite long, and longer than its subsequent counterparts, bearing constantly two superior nematothecae in a single row; remaining ahydrothecate internodes provided with commonly 1, or rarely 2, nematothecae. Hydrothecate internodes, up to 7 (usually 4-6) per cladium, relatively short, with a hydrotheca confined to most of their length (Fig. 3B), and up to four nematothecae: one mesial, a pair of laterals and, occasionally, an axillar one (Fig. 3E). Hydrothecae cup-shaped and shallow, walls slightly divergent, rim circular, entire (Fig. 3D, F). All nematothecae of the colony bithalamic and movable; mesial ones short, triangular in frontal view, rim of upper chamber with deep, adaxial emargination (Fig. 3G[3, 4]); laterals short, not surpassing the hydrothecal rim (Fig. 3D, F), and mounted on very short apophyses, conical in

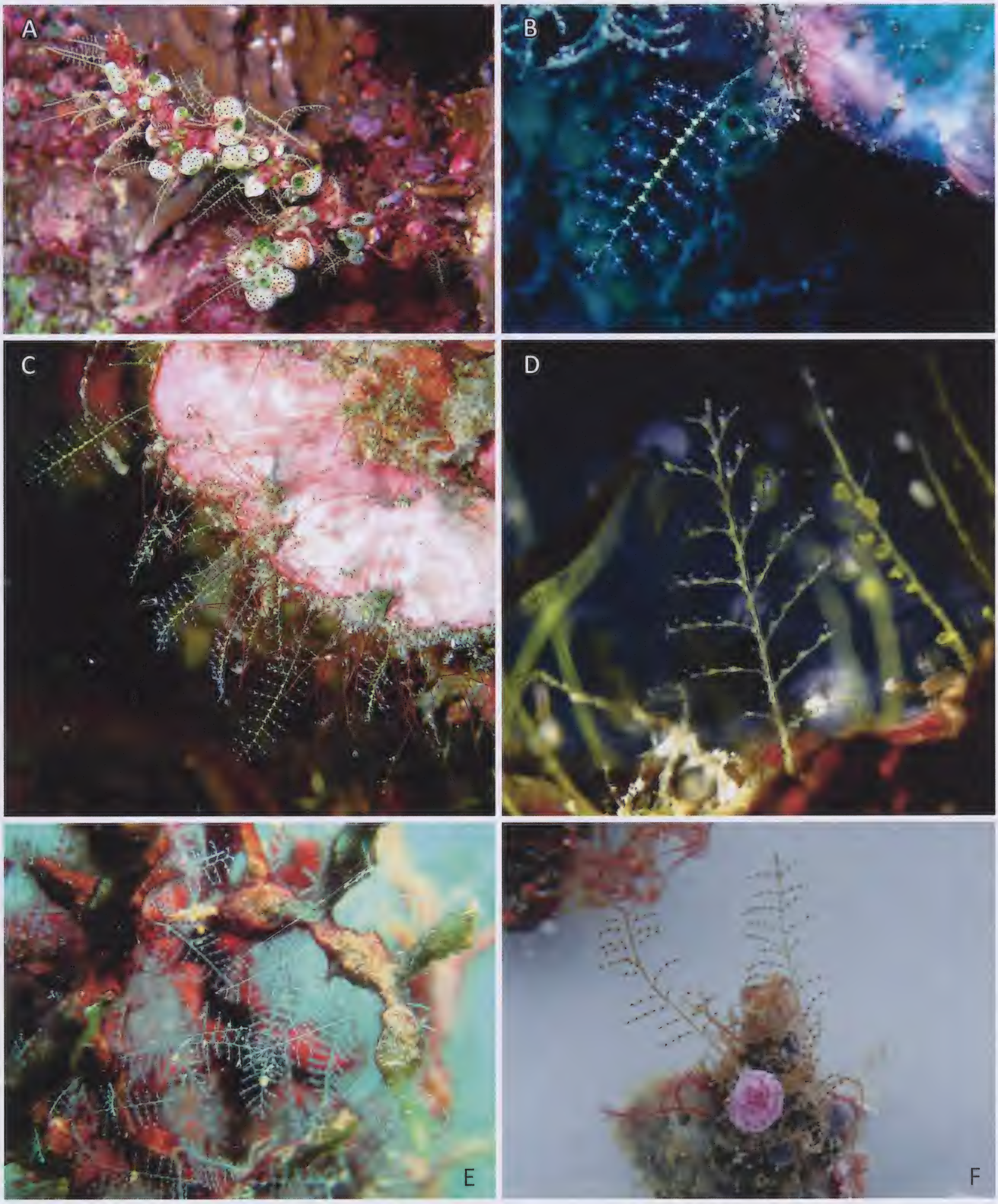


Fig. 1. Living colonies of *Halopteris* spp. showing their natural coloration. (A) *H. polymorpha* (Billard, 1913) from Bunaken, *in situ* (photo CGDC). (B, C) *H. sibogae* (Billard, 1913) from Bali, *in situ*. (D) *H. vervoorti* Galea, 2008 from the Maldives, *ex situ* (photo DM & SM). (E) *H. australis* sp. nov. from New Caledonia, *in situ*. (F) *H. millardae* sp. nov. from the Maldives, *ex situ* (photo DM & SM). Photos courtesy: N. & J-M. Bertot (B, C), E. Tardy (E).

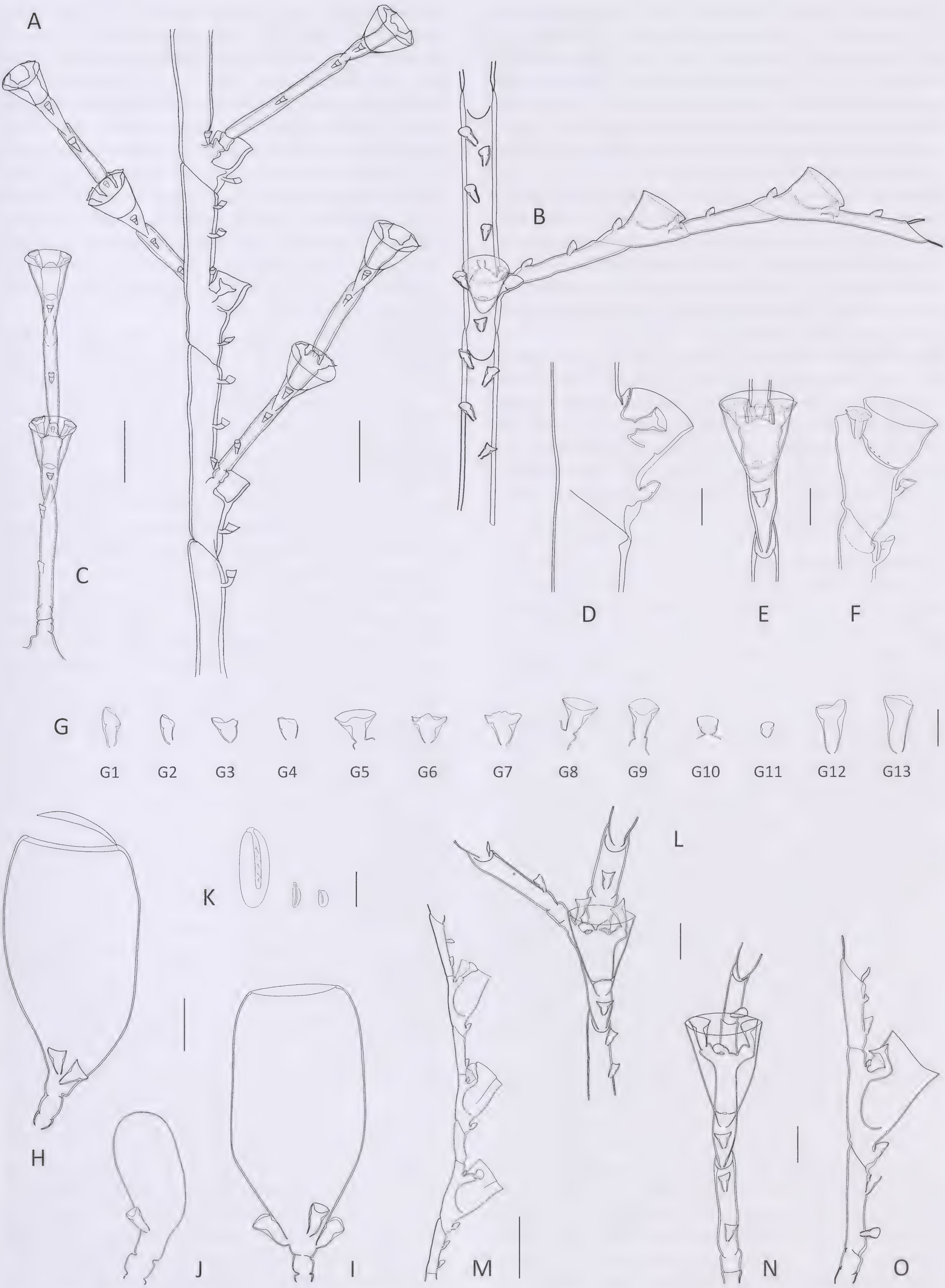
Fig. 2. Preserved cormoids of *Halopteris* spp. showing differences in their appearance. (A): *H. polymorpha* (Billard, 1913), MHNG-INVE-97937. (B): *H. sibogae* (Billard, 1913), MHNG-INVE-97938. (C-E): *H. vervoorti* Galea, 2008 from Bali (MHNG-INVE-97952), Toliara (MHNG-INVE-98633) and Martinique (HRG-0897), respectively. (F): *H. australis* sp. nov. (MHNG-INVE-82742). (G): *H. millardae* sp. nov., MHNG-INVE-98634. (H): *H. brasiliensis* sp. nov., MHNG-INVE-37495, slide H12/37. Scale bar: 5 mm.

shape, aperture wide, margin of upper chamber of variable shape: variously lowered to emarginated to sigmoid adaxially (Fig. $3G^{5-9}$); cauline (Fig. $3G^{1}$) and cladial (Fig. $3G^{2}$) nematothecae long, with tall basal and shallow upper chambers, rim scooped adaxially; axillar nematothecae conical to broadly ovoid, rather inconspicuous due to their comparatively smaller size and thinner perisarc (Fig. $3G^{10,\ 11}$). Hydranths with 15-16 filiform tentacles; in life, whole colony of a distinctive yellow tinge (Fig. 1A). Colonies dioecious. Gonothecae borne on both stems and cladia, inserted singly beside the base of a hydrotheca through a short, lateral apophysis, and mounted on single quadrangular pedicel; female large, broadly ovoid, tapering below, and there provided with 2-3 basal nematothecae; aperture distal, perpendicular to long axis of the theca, large and circular, with conspicuously thickened rim, closed by a watch-glass-shaped operculum (Fig. 3H, I); male comparatively smaller than female, ovoid, tapering below, without distinct aperture, provided basally with a couple of nematothecae (Fig. 3J). Cnidome (Fig. 3K) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(21.9-22.6) × (8.2-8.5) µm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(6.9-7.5) × *ca.* 2.4 µm, in tentacles]; small, ovoid capsules [(4.5-5.1) × (2.8-2.9) µm, scattered in the coenosarc].

Dimensions: See Table 1.

Remarks: The ordinary cauline internodes bear usually 2-3 nematothecae above their corresponding hydrothecae (60.8% and 34.8%, respectively, n=115), though exceptionally as few as 1, or as much as 4 or even 5, may occur (1%, 1.7% and 1.7%, respectively, n=115). The basalmost cauline internodes, supporting pairs of cladia, bear an increased number of nematothecae, usually 4-5. The ordinary cladial ahydrothecate internodes bear generally 1 and, less frequently, 2 nematothecae (92% and 8%, respectively, n=110).

Fig. 3. (A-K) *Halopteris polymorpha* (Billard, 1913). Portions of stems (A, B) and proximal part of a cladium (C). Stem (D) and cladial (E, F) hydrothecae, the latter in frontal and lateral views, respectively. Nematothecae (G) cauline (G^{1}), cladial (G^{2}), mesial from cauline (G^{3}) and cladial (G^{4}) hydrothecae, laterals from cladial hydrothecae (G^{5-9}), axillar from caulus (G^{10}) and cladium (G^{11}), and associated to the female gonotheca ($G^{12,\ 13}$). Female (H, I) and male (J) gonothecae. Cnidome (K).
(L-O) *Halopteris* sp. from *Siboga* Stn. 299, belonging to the syntype series of *Plumularia polymorpha* Billard, 1913. Cauline internode (L). Portion of a cladium (M), and the same much enlarged in frontal (N) and lateral (O) views. Specimens CDC004 (A, C, F), MHNG-INVE-97937 (B, D, E, $G^{1-7,\ 10,\ 11}$, H, K), HRG-0421 ($G^{8,\ 9,\ 12,\ 13}$, I, J), H.L. 1309 (L-O). Scale bars: 10 µm (K), 100 µm (D-G, L, N, O), 200 µm (H-J), 300 µm (A-C, M). ►


A
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Behind each cauline hydrotheca, there is large foramen for the passage of a nematophore, itself protected by a bithalamic nematotheca; the latter is occasionally lost, but the constant presence of the foramen in all internodes indicates the pre-existence of an axillar nematotheca. Conversely, the cladial hydrothecae bear only occasionally single axillar nematothecae, but their basal foramina are inconspicuous.

Terminal stolonization is quite common in the available samples, but no branched cladia have been observed.

The bulk of the syntype material of *H. polymorpha* (Billard, 1913) is housed in the collection of NBC but, due to important ongoing renovation works, could not be re-examined for the purpose of the present study (Koos van Egmond, *pers. comm.*).

However, the lectotype (from *Siboga* Stn. 80) – designated and well-illustrated by Schuchert (1997) – is distinctive through its long cauline and cladial ahydrothecate internodes, and its rather shallow hydrothecae, provided with short, conical lateral nematothecae borne on inconspicuous apophyses. The present material fully agrees with these, allowing an updated and more comprehensive account on *H. polymorpha* to be done.

A microslide (H.L.1309), stored in MNHN and containing a sterile cormoid from *Siboga* Stn. 299, was re-examined. The caulus is homomerously segmented, with the exception of its distalmost part, where transverse nodes intervene; each internode is moderately long and comprises a hydrotheca in its lower half, a lateral apophysis and up to 7 nematothecae (1 mesial, a pair of laterals, a pair of axillar, as well as 1-2 superior ones, a certain distance one above the other, and slightly displaced laterally to one another) (Fig. 3L). The hydrocladia are heteromerously segmented; the 1st ahydrothecate internode is longer than its subsequent counterparts, and bears generally 2 nematothecae (although 3 were noted in one instance); the ordinary ahydrothecate internodes are of a rather varied length and carry 1-2 nematothecae (Fig. 3M); the hydrothecate internodes bear a hydrotheca and its 4 associated nematothecae (1 mesial, a pair of laterals, and an axillar one) (Fig. 3N). All nematothecae, including the axillar ones, are bithalamic. The hydrothecae are deep and almost cylindrical, and their lateral nematothecae are mounted on well-developed apophyses, and scarcely reach the hydrothecal rim (Fig. 3O). Its gonothecae remain to be discovered.

Accordingly, it results that the material from *Siboga* Stn. 299 is morphologically different from the lectotype of *H. polymorpha* (compare Fig. 3A-F and 3L-O; see also Table 1), a finding that contrasts with earlier views expressed by both Billard (1913) and Schuchert (1997). The former material obviously belongs to a different, possibly an as yet unnamed species, whose comprehensive description requires additional, fertile material.

The 3rd morphotype belonging to the syntype of *H. polymorpha*, from *Siboga* Stn. 77, is presently the less documented (the available data are summarized in Table 4 herein). According to Billard (1913), its cladia, besides the proximal most, quadrangular segment, begin with an ahydrothecate internode provided with only one nematotheca, followed by a succession of "mostly" homomerously-segmented internodes bearing "most often" a single nematotheca. The rather deep hydrothecae, provided with lateral nematothecae borne on well-developed apophyses, combined with the structure of the hydrocladia, suggest – with little doubt – that the material from *Siboga* Stn. 77 is specifically different from both the lectotype of *H. polymorpha* and the material in hand described above, thus contradicting – again – the opinions expressed by both Billard (1913) and Schuchert (1997).

Halopteris nuttingi (Billard, 1911) was synonymized with *H. polymorpha* by Schuchert (1997), an opinion not shared here. However, we agree with him that its inclusion in the synonymy of *H. buskii* (Bale, 1884), proposed by Billard (1913), is not justified as they have morphologically different gonothecae. According to Billard (1913), *H. nuttingi* [as *Plumularia buski* (*sic!*)] and *H. polymorpha* could be confidently distinguished through the shape of the upper chamber of their lateral nematothecae: globular with distinctly emarginated ad- and abaxial walls in the former, and conical with slight adaxial emargination in the latter (it was stated above that the complete panoply of shapes displayed by the latter also include a sinuated rim or an adaxial emargination). In Schuchert's (1997) view, this character is unreliable, arguing that in other halopteridids, *e.g. Antennella quadriaurita* Ritchie, 1909, "it is notoriously variable". However, since then, it has been suggested that the former concept of *A. quadriaurita* likely includes a complex of species (Galea, 2013: 29), and it has been demonstrated, for instance, that at least one "morphotype" represents a distinct, well-characterized species (Galea & Ferry, 2015: 237). Moreover, besides the distinctive shape of the lateral nematothecae, the number and position of their counterparts confined to the cauline internodes distal to hydrotheca is different in *H. nuttingi* (see Billard, 1913). Last but not least, according to both Billard (1911, fig. 8; 1913, fig. 11) and Schuchert (1997, fig. 21C), this nominal species has shorter cladial ahydrothecate internodes and deeper hydrothecae compared to *H. polymorpha*.

Additionally, it should be stressed that *H. nuttingi* was created based on a syntype, as it results from Billard's [1913, as *Plumularia buski* (*sic*!) Bale, 1884] work, but not from his original account (Billard, 1911). Moreover, according to the former publication, it is very likely that the syntype contains a mix of species, as Billard mentions (p. 22) ahydrothecate cladial internodes either short or long, and provided with one or two nematothecae. However, a neotype (*sic*!) for *H. nuttingi* has been designated (Coel. 5241) by Schuchert (1997: 64), who also provided reliable illustrations of it (N.B.: This material should be best referred to as the lectotype). Besides Billard's (1911, 1913) record of *H. nuttingi*,

at least two others seem to occur in the literature, *viz.* Redier [1966: 90, pl. 2 figs 1 & 3, pl. 3 fig. 1; as *P. buski* (*sic!*)] and Watson (2000: 46, fig. 35C, E; *pro parte* as *H. polymorpha*).

Literature records of *H. polymorpha* are a matter of debate, due to several main factors: 1) the lack of formal descriptions, or descriptions too succinct, sometimes not accompanied by illustrations, a situation mainly occurring in older literature; 2) only sterile material was available, thus generating confusion with *H. buskii* (Bale, 1884); 3) the artificial inclusion in the synonymy of Billard's (1913) species of a variety of hydroids displaying a large panoply of morphological features, the specific name "*polymorpha*" being obviously misleading. Schuchert (1997) and Ansín Agis *et al.* (2001, 2009) provided extensive lists of synonyms for this taxon (a compilation is given in the synonymy above), though only a few prove reliable in light of the present observations.

For instance, the material studied by Di Camillo *et al.* (2008) and re-examined herein, belongs to the present species. In addition, the Fijian record by Ryland & Gibbons (1991: 530) is also in agreement with it, since it displays the distinctively long cladial ahydrothecate internodes, relatively shallow hydrothecae, lateral nematothecae (with flared upper chamber) borne on inconspicuous apophyses, as well as the occasional presence of axillar nematothecae behind the cladial hydrothecae (it is assumed that their cauline counterparts were overlooked by the authors). Although neither formally described, nor illustrated, the Queensland record by Pennycuik (1959) is reportedly said similar with Billard's fig. 14A, presently known as representing the lectotype of *H. polymorpha*.

Besides these few records, many others clearly deviate morphologically from the lectotype. Among them, there are morphotypes characteristically forming either tall (> 4 cm high) or small-sized (< 2 cm high) cormoids. Specimens with tall stems were described, for instance, in materials from South Africa (Millard, 1975), Zanzibar (Rees & Vervoort, 1987; as *H. buskii*), and the Seychelles (Millard & Bouillon, 1973). Millard's (1975) material is, obviously, a mix of species: one with very deep, almost tubular hydrothecae (her fig. 112K), while the other (her fig. 112L) corresponds morphologically to the redescription of the lectotype of *H. buskii* provided by Schuchert (1997). Conversely, the specimens from Zanzibar and the Seychelles (part of the latter re-examined herein) belong to an as yet undescribed species, *Halopteris millardae* (see below).

On the other hand, among the materials with small-sized cormoids, several morphological groups could be distinguished. First, there are specimens whose hydrothecae distinctly display sinuated margins (Vervoort & Vasseur, 1977), and these belong to the new species, *Halopteris australis*, described below. Second, there are materials whose hydrothecae possess an even rim, but further divide into a subgroup with homomerously-segmented cladia (*e.g.* Vervoort, 1966; Hirohito, 1983) and another one displaying a heteromerous division into internodes [*e.g.* Vervoort (1967), as *Antennella secundaria*; Hirohito (1974), as *Heterotheca buski* (*sic!*); Ryland & Gibbons (1991), as *H. buskii*; Hirohito (1995), as *H. buski* (*sic!*); Preker & Lawn (2010, 2012)]. Some specimens, among the materials with heteromerous cladia, are thought to belong to *H. vervoorti* Galea, 2008 (see below under this species), while the taxonomic status of the remaining ones is uncertain in light of the available data (see Tables 2 and 4). The reexamination of extant specimens, the availability of newly-collected materials, as well as modern, molecular approaches are expected to gradually solve the intricacies of this species group.

A sample provisionally identified as *H. polymorpha*, originating from the Mediterranean, was first used in a molecular phylogeny by Leclère *et al.* (2007). The voucher specimen used in that work (MHNG-INVE-30117, data in Appendix 2) was re-examined for the purpose this study. The single cormoid is sterile and thus not reliably identifiable. It resembles *H. vervoorti*, notably in having pairs of axillar nemathothecae associated to the cauline hydrothecae. More and especially fertile material is needed for a correct identification, as it likely belongs to an as yet undescribed species, according to the 16S data (Fig. 9; DQ855922).

Halopteris polymorpha, as presently understood, can be separated from its congeners [see list in Schuchert (2015)] through a series of morphological features. The following hydroids can be excluded *a priori* from the comparison, on the account of a series of diagnostic traits which separate them easily from the species discussed here:

1) the fascicled habit of their stems [occasional in *H. campanula* (Busk, 1852), common in *H. valdiviae* (Stechow, 1923)];
2) their cladia arranged in opposite pairs [*H. catharina* (Johnston, 1833), *H. clarkei* (Nutting, 1900), *H. enersis* Galea, 2006, *H. gemellipara* Millard, 1962, *H. geminata* (Allman, 1877), *H. opposita* (Mulder & Trebilcock, 1911), *H. plagiocampa* (Pictet, 1893), *H. prominens* Vervoort & Watson, 2003];
3) their gutter-shaped hydrothecae [*H. everta* (Mulder & Trebilcock, 1909)], or 4) their hydrothecae divided by internal septa [*H. diaphragmata* (Billard, 1911), *H. jedani* (Billard, 1913)], or
5) provided with either an abaxial cusp (*H. rostrata* Millard, 1975) or
6) a longitudinal carina (*H. carinata* Allman, 1877);
7) the presence of two pairs of lateral nematothecae (*H. infundibulum* Vervoort, 1966).

As to the remaining species, their differences to *H. polymorpha* are summarized in Appendix 1.

Among them, according to the phylogenetic tree shown in Fig. 9, *H. polymorpha* comes close to *H. platygonotheca* Schuchert, 1997. Besides notable differences in their respective female gonothecae (pear-shaped in the former, and conspicuously laterally-flattened in the latter), their trophosomes display several common characters: 1) their stem internodes are long and provided with several

nematothecae distal to the hydrothecae [commonly 2-3 (but up to 5 possible) in *H. polymorpha*, and from 1 (sample MHNG-INVE-97943) to 1-3 (sample HRG-1288) in *H. platygonotheca*]; 2) the occurrence (regular in the former and occasional in the latter) of an axillar nematotheca behind the cauline hydrothecae; 3) their cladial ahydrothecate internodes are long; 4) the apophyses supporting their lateral nematothecae are inconspicuous, and the thecae themselves do not reach the hydrothecal rim.
Taken together, the previous supposed morphological variability of, and the implicit difficulty in establishing a specific limitation in *H. polymorpha*, are now solved through the discovery of additional records in perfect agreement with the lectotype designated by Schuchert (1997). It is concluded that Billard's (1913) species is well-characterized and morphologically homogenous, as illustrated with the present material belonging to various geographically-distant Indonesian populations.

Distribution: Scattered records from Indonesia, *viz.* off Kalimantan (Billard, 1913, *Siboga* Stn. 80), Bali and Ambon (present study), Bunaken National Park (Di Camillo *et al.*, 2008; present study). Also occurring in Fiji (Ryland & Gibbons, 1991). A doubtful record from Queensland, Australia (Pennycuik, 1959).

Halopteris sibogae (Billard, 1913)

Figs 1B-C, 2B, 4; Table 1; Appendix 1

Plumularia polymorpha var. *sibogae* Billard, 1913: 25, fig. 16. – Van Soest, 1976: 89.
Thecocaulus polymorphus var. *sibogae* – Bedot, 1921: 9. – Stechow, 1925: 497.
Halopteris polymorpha var. *sibogae* – Millard & Bouillon, 1973: 84, fig. 10K. – (?) Hirohito, 1983: 62; 1995: 244.
Halopteris polymorpha – Schuchert, 1997 (*pro parte*): 66, 69, fig. 22E [non *Halopteris polymorpha* (Billard, 1913)].

Material examined: MHNG-INVE-97926; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.27417° 115.59265°, 22 m, coll. H. R. Galea; 29.09.2016; numerous plumes up to 23 mm high, of which many bear male gonothecae; 16S sequence MF784526. – MHNG-INVE-97938; Indonesia, Bali, Padangbai, Jepun shipwreck, -8.52812° 115.51478°, 20 m, coll. H. R. Galea; 06.10.2016; numerous plumes up to 25 mm high, of which 2 bear female gonothecae; 16S sequence MF784531. – HRG-0991; Indonesia, Tukang Besi Archipelago, reef north off Hoga I., -5.44633° 123.76417°, 20 m, coll. G. Allard; 27.09.2011; several infertile plumes up to 20 mm high.

Diagnosis: *Halopteris* with cormoids reaching heights of up to 2.5 cm, with monosiphonic, unbranched stems, divided homomerously into short internodes bearing a hydrotheca, a lateral apophysis, and up to 8 nematothecae (1 mesial, a pair of laterals, 1-2 axillary ones, and commonly 2-3 above hydrotheca). Cladia alternately arranged along stem, heteromerously divided into internodes; hydrothecate internodes longer than their ahydrothecate counterparts, carrying a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and 1-2 axillary ones); ahydrothecate internodes short, provided with 1-2 nematothecae. Hydrothecae deep, almost tubular. Lateral nematothecae borne on well-developed apophyses; basal chamber tall, whole nematotheca greatly surpassing hydrothecal margin; rim of upper chamber with adaxial emargination. Female gonotheca broadly ovoid, with large, rounded, apical aperture perpendicular to long axis of the theca, and closed by glass-watch-shaped operculum; 3 basal nematothecae. Male gonotheca smaller than female, ovoid, without noticeable aperture, with 2 basal nematothecae. In life, cauline polyps yellow, contrasting with their purely white cladial counterparts.

Description: Colonies composed of numerous cormoids arising from tubular, creeping, branching hydrorhiza lacking nematothecae. Cormoids erect (though flaccid when out of liquid), up to 2.5 cm high. Cauli simple, monosiphonic (Figs 1B-C, 2B), from straight in their lower halves to distinctly geniculate in their upper halves; basal parts of varied length (1-11 mm long), rarely entire, generally subdivided into segments by a number of transverse nodes (up to 4 observed); segments ahydrothecate, but carrying a total of 0-43 nematothecae arranged in two distinct, longitudinal, closely-set rows; distal end of last segment marked by deeply-cut, oblique node. Remainder of stem longer, with strict homomerous segmentation; each cauline internode (Fig. 4A) moderately-long, bearing a hydrotheca in its lower half, a number of nematothecae, as well as at least a short, lateral apophysis supporting a cladium; up to 33 successive internodes observed. The proximal most internode bears always two opposite apophyses supporting a pair of cladia, but there may be up to 3 consecutive segments displaying this feature; all are demarcated by deeply-incised, oblique nodes, both proximally and distally. Above, the segments are separated by less-marked, oblique constrictions of the perisarc, and each bears but a single apophysis originating laterally next to the hydrotheca; apophyses alternate along the stem. There are 6-9 nematothecae per internode, of which 4-5 are associated to the hydrotheca: 1 mesial, a pair of laterals, 1-2 axillar, as well as 2-4 superior ones arranged in two parallel rows (Fig. 4A); all cauline nematothecae, exclusive of those associated to the hydrothecae, tightly and backwardly appressed against stem (turned posteriad), at least in preserved material. Cladia up to 3 mm long; composed of a very short, proximal, quadrangular, athecate segment, followed by a succession of alternating ahydrothecate and hydrothecate internodes (Fig. 4A, C); ahydrothecate internodes with proximal transverse node and oblique distal node; the reverse in hydrothecate internodes. First ahydrothecate internode

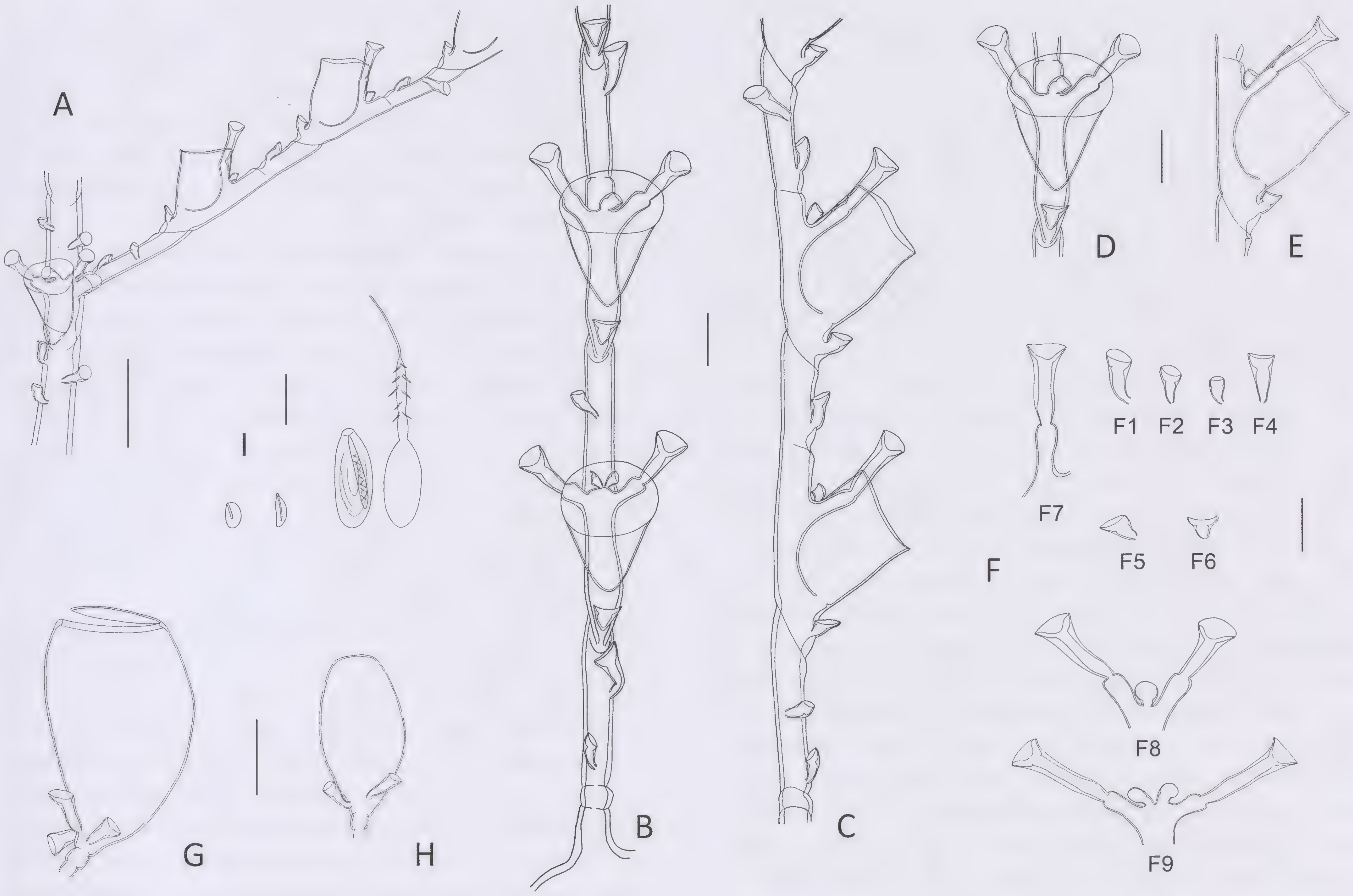

Fig. 4. *Halopteris sibogae* (Billard, 1913). Portion of stem and proximal part of a cladium in frontal (B) and lateral (C) aspects. Hydrotheca in frontal (D) and lateral (E) views. Cladial nematothecae (F): from ahydrothecate internodes (F^{1-4}), mesial ($F^{5,6}$), lateral (F^{7}), single (F^{8}) and paired (F^{9}) axillar ones. Female (G) and male (H) gonothecae. Cnidome (I). Specimens MHNG-INVE-97938 (A-G, I), MHNG-INVE-97926 (H). Scale bars: 10 µm (F), 100 µm (D, E, I), 200 µm (G, H), 300 µm (A-C).

comparatively longer than following counterparts, and always carrying 2 nematothecae in a row; remaining internodes with either 1 or 2 nematothecae in a row. Hydrothecate internodes, up to 8 per cladium, relatively short, accommodating a hydrotheca in their lower 3/4th and its 4-5 associated nematothecae: 1 mesial, a pair of laterals, and 1-2 axillar (Fig. 4B, D). Hydrothecae cup-shaped and relatively deep, adnate for half their length to corresponding internode, free adaxial and abaxial walls parallel, flaring slightly to margin; the latter circular in apical view, and slightly sigmoid laterally, with imperceptible scoop between side facing the lateral nematothecae and abaxial wall (Fig. 4C, E). All nematothecae, including the axillar ones, bithalamic and movable. Mesial ones triangular in frontal view, upper chamber with conspicuously lowered margin on adaxial side (Fig. $4F^{5,6}$). Lateral nematothecae mounted on well-developed apophyses (Fig. $4F^{7}$); long, greatly surpassing the hydrothecal rim (Fig. 4C, E), lower chamber high, upper one relatively shallow, and with adaxial emargination. Axillar nematothecae cornucopia-shaped, adaxial wall of upper chamber with significant emargination (Fig. $4F^{8,9}$). Remaining nematothecae from both caulus (not shown) and cladia (Fig. $4F^{1-4}$) similar to the lateral ones, though comparatively shorter. Hydranths with 13-15 filiform tentacles; in life, all belonging to the stem characteristically yellow, contrasting with those from the cladia that are uniformly white (Fig. 1C). Colonies dioecious. Gonothecae arising laterally from below the stem hydrothecae through a short, lateral apophysis; mounted on short, quadrangular pedicel, broadly ovoid, though sexually dimorphic, with the males comparatively smaller than females; the latter provided basally with 3 nematothecae similar to the laterals of the hydrotheca, and a large, watch-glass-shaped apical lid closing a rounded aperture with conspicuously thickened perisarc at margin (Fig. 4G); male gonothecae bearing two basal nematothecae and no noticeable aperture; a globular mass of sperm cells encircles a central, digitiform blastostyle (Fig. 4H); all female gonothecae observed ripe and empty, with the exception of basal remains of the blastostyle. Cnidome (Fig. 4I) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(18.1-19.8) × (6.6-7.3) µm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(6.1-6.6) × (2.1-

2.3) µm, in tentacles]; small, ovoid capsules [(5.1-5.4) × (2.9-3.1) µm, scattered in the coenosarc].

Dimensions: See Table 1.

Remarks: In most stems, the proximal most hydrothecate internode gives rise to a pair of cladia; occasionally, two successive internodes are involved; in one instance, three proximal pairs occurred, followed by an internode provided with a single apophysis, and by another one giving rise to a pair of cladia. In such internodes, there are always 3 or even 4 nematothecae above the hydrotheca. The remaining stem internodes are randomly provided with either 2 or 3 nematothecae in two parallel rows. Both cauline and cladial hydrothecae bear either one (70% and 80% of cases, respectively, n=50 examined hydrothecae) or two (30% and 20% of cases, respectively) axillar nematothecae.

Terminal stolonization occurs occasionally from the distal ends of both stems and cladia. Rarely, aberrant branching of cladia occurs: a short apophysis is given off laterally from either one or both apophyses supporting the lateral nematothecae; the structure of these 2nd order branchlets (not exceeding two hydrothecate internodes) is similar to that of a normal cladia, and begins with a short, quadrangular, athecate segment, followed by the first ahydrothecate intersegment carrying but a single nematotheca, instead of two as in the 1st order cladia.

Sterile cormoids, similar to the present ones, with hydrothecae provided with exceedingly long lateral nematothecae were already reported notably from Indonesia by Billard (1913) and the Seychelles by Millard & Bouillon (1973) (both as *Halopteris polymorpha* var. *sibogae*). According to the former author, this character mainly distinguishes his so-called variety from the nominal species.

Similarly to the present observations, Millard & Bouillon indicate that "Intermediate athecate internodes [are] absent on stem but invariably present on hydrocladia", although Billard observed that, on cladia, the ahydrothecate internodes may be occasionally fused to their preceding hydrothecate counterparts. Among the quite rich material studied here, only one case of fusion (Fig. 4B, after the proximal most hydrotheca) was noted upon the careful examination of 10 cormoids from sample MHNG-INVE-97938.

As noted above, the most prominent morphological difference between *H. polymorpha* and its so-called variety *sibogae* is to be found in the shape and size of their lateral nematothecae, including their corresponding apophyses (compare Fig. 3D-F and 4B-E). Another noteworthy difference relies in the comparatively shallower hydrothecae (compare Fig. 3D & E and 4C & E), and shorter cauline (compare Fig. 4A and 3A-B) and cladial ahydrothecate (compare Fig. 4C and 3B) internodes in the former. Moreover, only noticeable in living material, the bicolor aspect of the cormoids of the latter is striking (Fig. 1B, C), compared to the wholly yellow tinge observed in the former (Fig. 1A), especially when both species occur in sympatry. Other morphological and morphometrical differences observed in the material studied herein are listed in Table 1. In light of these differences, we advocate here that the so-called variety *sibogae* must be recognized as a full species, different from *H. polymorpha*. The 16S data clearly corroborated this (Fig. 9).

Raising *Plumularia polymorpha* var. *sibogae* Billard, 1913 to full species is not threatened by *Plumularia sibogae* Billard, 1911, because the former is to be correctly placed in the genus *Halopteris* Allman, 1877 [as *H. sibogae* (Billard, 1913)], while the latter is accommodated in *Antennella* Allman, 1877.

Halopteris sibogae differs from its congeners through a series of characters. A number of species with "peculiarities" (see under *H. polymorpha*) should be excluded from the comparison, while the remaining ones are compared in Appendix 1.

Among them, and in accordance with the phylogenetic tree, *H. sibogae* comes close to *H. vervoorti* Galea, 2008 (see below an account on the latter). Besides its exceedingly long, and thus very distinctive, lateral nematothecae, *H. sibogae* shares the following features with *H. vervoorti*: 1) their cauline internodes are rather short and bear 1-2 nematothecae distal to each hydrotheca; 2) there are 1-2 axillar nematothecae associated to both cauline and cladial hydrothecae; 3) their cladia are heteromerously-segmented, their ahydrothecate internodes are short compared to their hydrothecate counterparts, and bear single nematothecae; 4) their female gonothecae are indistinguishable morphologically (compare Fig. 4G and 5H, I, P).

Distribution: Indonesia [between Misool I. and West Papua (Billard, 1913), Bali (present study), Tukang Besi Archipelago (present study)], Seychelles (Millard & Bouillon, 1973), and questionably Japan (Hirohito, 1983).

Halopteris vervoorti Galea, 2008

Figs 1D, 2C-E, 5; Tables 3, 4; Appendix 1

Halopteris vervoorti Galea, 2008: 42, fig. 9; 2010: 3, 4; 2013: 50.

Halopteris polymorpha – Ansín Agís *et al.*, 2001: 167, fig. 70. – (?) Preker & Lawn, 2010: 120 [non *Plumularia polymorpha* Billard, 1913 (*pro parte*): 24, fig. 14B, C].

Heterotheca buski – (?) Hirohito, 1974: 30, fig. 14 (incorrect subsequent spelling).

Halopteris buskii – (?) Ryland & Gibbons, 1991: 527, fig. 2.

Halopteris buski – (?) Hirohito, 1995: 244 fig. 82 (incorrect subsequent spelling).

non *Plumularia buskii* Bale, 1884: 125, pl. 10 fig. 3, pl. 19 figs 34-35.

Antennella secundaria – (?) Vervoort, 1967: 42, fig. 12 [non *Antennella secundaria* (Gmelin, 1791)].

Material examined: MHNG-INVE-98635; Republic of Maldives, Faafu Atoll, Magoodhoo Island, 3.07606°

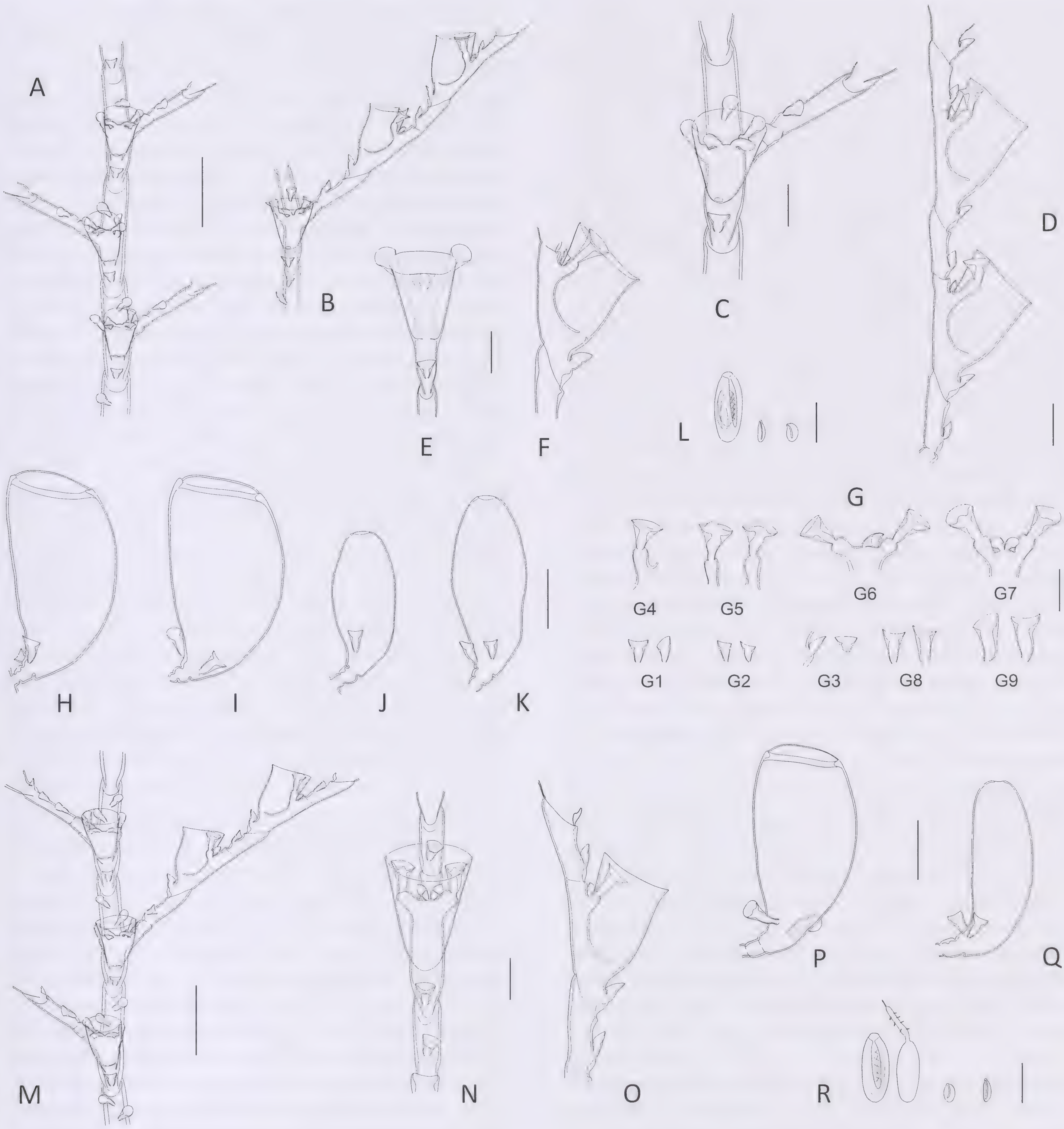

Fig. 5. *Halopteris vervoorti* Galea, 2008 from the Indian Ocean (A-K) and the Caribbean (M-R). Portions of stems with cladia (A, B, M). Cauline internode (C). Portion of cladium, enlarged (D). Hydrothecate internodes in frontal (E, N) and lateral (F, O) aspects. Nematothecae (G): from caulus (G^1) and cladia (G^2), mesial (G^3) and laterals ($G^{4,5}$) from cladial hydrothecae, single (G^6) and paired (G^7) axillar associated to cladial hydrothecae. Female (H, I, P) and male (J, K, Q) gonothecae. Cnidomes (L, R). Specimens MHNG-INVE-98635 (A, C, G^7), MHNG-INVE-97952 (B, F, $G^{4,6}$, L), MHNG-INVE-98633 (D, E, $G^{1-3,5,8,9}$, H-K), HRG-1339 (M, P), HRG-0897 (O), HRG-0337 (Q, R). Figure in N is reproduced after Galea (2008). Scale bars: 10 µm (L, R), 100 µm (C-G, N, O), 200 µm (H-K, P, Q), 300 µm (A, B, M).

72.96159°, 3 m, coll. D. Maggioni and S. Montano; 29.01.2016; many stems, up to 1.3 cm high, some of them bearing female gonothecae; 16S sequence MF773743. – MHNG-INVE-98636; Republic of Maldives, Faafu Atoll, 3.07478° 72.96628°, 10 m, coll. D. Maggioni and S. Montano; 13.04.2016; 4 stems, 5-7 mm high, of which one bears two young female gonothecae; 16S sequence MF773742. – MHNG-INVE-97952; Indonesia, Bali, Pemuteran, -8.14338° 114.65805°, 0.5 m, coll. H.R. Galea; 04.10.2015; several sterile cormoids, up to 1.2 cm high. – MHNG-INVE-98633; Madagascar, Bay of Toliara, Dimadimatsy reef, -23.48234° 43.73285°, 1-2 m, coll. N. Gravier-Bonnet; 13.09.1969; fertile (monoecious) colony on alga, stems up to 0.8 cm high. – HRG-0337; France, Guadeloupe, Basse-Terre, Petite Anse, 16.09639° -61.77139°, 0-1 m, coll. H.R. Galea; 22.01.2008; numerous cormoids, up to 1.2 cm high, some bearing male gonothecae. – HRG-0897; France, Martinique, Case-Pilote, 14.64311° -61.14171°, 5-7 m, coll. H.R. Galea; 27.02.2014; several infertile plumes, up to 1.3 cm high. – HRG-1339; France, Martinique, Case-Pilote, 14.64337° -61.14199°, 1-2.5 m, coll. R. Ferry; 24.07.2017; numerous cormoids, up to 1.9 cm high, many bearing male gonothecae, and one their female counterpart; 16S sequence MF773741. – DM&SM-CU005; Dutch Caribbean, Curaçao I., Piscadera Bay, 12.12139° -68.96917°, 11 m, coll. S. Montano; 09.06.2017; two sterile stems, *ca.* 15 mm high; 16S sequence MF773740.

Diagnosis: Small-sized (up to 2.0 cm high) *Halopteris* with homomerously-divided stems; internodes rather short, comprising a hydrotheca in their lower 2/3rd part, a well-developed lateral apophysis, and up to 7 nematothecae (1 mesial, a pair of laterals, 2 axillar, and 1-2 superior ones in a median row). Cladia alternate, divided heteromerously; hydrothecate internodes comparatively longer than their ahydrothecate counterparts, bearing a centrally-placed hydrotheca and up to 5 nematothecae (1 mesial, a pair of laterals and generally 1, exceptionally 2, axillar nematothecae); ahydrothecate internodes very short, carrying single nematotheca in their lower halves. Hydrotheca deep, tubular, slightly flaring below aperture, rim circular, slightly scooped in lateral view. Lateral nematothecae barely surpassing hydrothecal rim, borne on well-developed apophyses; conical, walls of lower chamber gradually thickening distally, apical chamber shallow, rim from lowered to sinuated adaxially. Male gonothecae elongated-ovoid, borne on short, quadrangular pedicel; 2 basal nematothecae; distally a narrow, circular aperture. Female gonothecae comparatively larger, borne on short, quadrangular pedicel; broadly ovoid, tapering below, with large apical aperture with thickened rim, closed by glass-watch-shaped operculum; basally 2-3 nematothecae.

Description: Colonies composed of varied number of cormoids arising from tubular, creeping, branching hydrorhiza, devoid of nematothecae. Stems simple, erect (up to 13 mm high in present material), monosiphonic (Figs 1D, 2C-E), composed of a basal, ahydrothecate part, and a much longer, distal part bearing hydrothecae and cladia. Basal part of varied length, almost straight, irregularly divided into successive segments of unequal length through up to 6 transverse nodes, bearing a total of up to 18 nematothecae arranged in two parallel, closely-set, longitudinal rows; distalmost segment separated from hydrothecate part of caulus through deeply-incised, oblique node. Upper part of caulus almost collinear proximally, becoming decidedly geniculate distally, divided into up to 15 regular internodes by means of oblique nodes (Fig. 5A, M); distally, the segmentation may occasionally change to heteromerous through the insertion of transverse nodes. Each stem internode composed of a hydrotheca situated in its proximal half, a lateral apophysis (or a pair in the proximal most internode), and up to 7 nematothecae (a mesial, a pair of laterals, a pair of axillar, as well as 1 or, occasionally, 2 superior ones in a median row (Fig. 5C); superior nematothecae confined to a separate, ahydrothecate internode, where caulus segmentation becomes heteromerous; often a pair of laterally-displaced superior nematothecae, inserted at same level, on proximal most stem internode bearing the pair of cladia); internodes slightly bent above hydrotheca in opposite direction to corresponding cladium. Apophyses, exclusive of those of proximal most internode (that are paired), alternate along stem, each supporting a cladium. Cladia composed of a proximal, short, athecate, quadrangular internode, followed by a succession of a- and hydrothecate internodes resulting through a heteromerous segmentation (Fig. 5B). Ahydrothecate internodes with transverse proximal node and oblique distal node, carrying proximally a single nematotheca; internodes very short, though proximal most one slightly longer than subsequent counterparts (Fig. 5D). Hydrothecate internodes, up to 4 per cladium, with oblique proximal node and transverse distal node, rather short, accommodating a centrally-placed hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, as well as 1, or exceptionally 2, axillar nematothecae) (Fig. 5E, N). All hydrothecae deep, conical, adnate for about half their adaxial length; free adaxial wall straight, abaxial wall slightly sigmoid (basally imperceptibly concave, distally slightly everted below rim); aperture wide, circular, rim slightly scooped in lateral view (Fig. 5F, O); hydranths with *ca.* 14 filiform tentacles. Gonothecae borne on both caulus and cladia through short, lateral apophyses arising midway between hydrothecal bases and mesial nematothecae. Female gonothecae large, piriform, borne on short quadrangular pedicels; basally a couple of nematothecae; distally a large, ovoid, transverse aperture, with conspicuously thickened rim, closed by

a glass-watch-shaped operculum (Fig. 5H, I, P). Male gonothecae borne on single, quadrangular pedicels; fusiform to elongated-ovoid, with couple of basal nematothecae, and a distal, narrow, circular, transverse aperture, closed by thin perisarc sheet (Fig. 5J, K, Q). All nematothecae bithalamic, including the axillar ones; mesial triangular in frontal view, upper chamber slightly shallower than basal one, with conspicuously lowered rim on adaxial side (Fig. $5G^3$); laterals borne on well-developed apophyses, conical, moderately-long (Fig. $5G^{4,5}$), not always reaching the hydrothecal rim (Fig. 5D, F, O); basal chamber narrow, tubular, rather tall; upper chamber shallow, wide, margin either lowered or sigmoid on adaxial side; cauline (Fig. $5G^1$) and cladial (Fig. $5G^2$) nematothecae, other than those associated to the hydrothecae, as well as those borne by the gonothecae (Fig. $5G^{8,9}$), long conical, with tall basal chamber and comparatively shallow upper chamber, with rim slightly lowered adaxially; axillar nematothecae (Fig. $5G^{6,7}$) with much thinner perisarc than their exposed counterparts, short, with chambers of nearly the same depth, wall of upper chamber facing adaxial hydrothecal wall distinctly lowered. Cnidome (Fig. 5L, R) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(16.8-18.2) × (6.5-6.8) µm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(5.6-5.8) × (1.9-2.1) µm, in tentacles]; small, ovoid capsules [(4.5-4.9) × (2.8-2.9) µm, scattered in the coenosarc]. Color in life from pale yellow to brownish.

Remarks: The segmentation of cauli is generally homomerous, although the insertion of transverse node towards their distal parts introduces a heteromerous segmentation. The cladia are generally divided heteromerously, though an occasional absence of transverse nodes could be noted in material MHNG-INVE-98635, this not supposing a homomerous segmentation throughout the involved cladium. The cauline hydrothecae generally display a pair of axillar nematothecae, though only one, placed medially, may occasionally occur in distalmost hydrothecae. In contrast, generally a single axillar nematotheca is associated to each cladial hydrotheca though, exceptionally, a couple may occur. The stems internodes bear generally 1, occasionally 2, median superior nematothecae (*ca.* 95% and 5%, respectively, n=150); these are arranged in a single row in ordinary internodes, while they are shifted laterally and occur at the same level in the basalmost internodes giving rise to pairs of cladia. The first cladial internodes bear generally but a single nematotheca; rarely, two nematothecae were observed in some cormoids from MHNG-INVE-98635. The material MHNG-INVE-9833 comprises monoecious stems, while only female gonothecae seem to occur in former.

The trophosomes of the present materials from the Indian Ocean were compared with those of specimens from the Lesser Antilles, and all appear indistinguishable, both morphologically and morphometrically (compare Fig. 5A, B, D and 5M, O). In addition, the as yet unknown female gonothecae of the Caribbean population, were found only recently (sample HRG-1339), and do not differ from those of the Indian Ocean counterparts (compare Fig. 5P and 5H & I; Table 3). Moreover, the molecular study supports the conclusions based on the morphological observations (Fig. 9).

Several literature records of hydroids conform, through the segmentation of both the stem and cladia, and the number and position of the nematothecae they carry, to the morphology of the present species. However, minor discrepancies could be occasionally noted, although they are thought to reflect rather overlooked details. Thus, Vervoort's (1967) material from the Red Sea, obviously erroneously assigned to *Antennella secundaria* (Gmelin, 1791), is reportedly said to carry single axillar nematothecae behind the cauline hydrothecae, a situation – indeed – met with only distally in the stems of the present species. Moreover, it should be stated that one nematotheca belonging to a pair, namely that given off on the same side as the corresponding cladium, may be difficult to notice as it is hidden (in frontal view) by the apophysis supporting the lateral nematotheca originating on the same side (see Fig. 5C – lateral nematotheca on same side as the cladium expressly shown).

The "second pair of lateral nematothecae [...] mesial to and much smaller than normal pair", observed by Ryland & Gibbons (1991) in their Fijian specimens assigned to *H. buskii*, is nothing else than the couple of cauline axillar nematothecae. Similarly so, besides the commonly seen single cladial axillar nematothecae, "two medio-superior nematothecae are often present behind the free adcauline wall of the hydrotheca". These, combined to the heteromerous segmentation of cladia, the shape and size of both hydro-and lateral nematothecae, and the morphology of the female gonotheca, suggest that their specimens are, most probably, conspecific with *H. vervoorti*.

The Japanese materials assigned to both *Heterotheca* and *Halopteris buski* (*sic!*) by Hirohito (1974, 1995, respectively) are morphologically close to the present species, as their cauli and cladia display the same segmentation, the same number and position of nematothecae, and the monoecious condition of their cormoids. However, a pending genetic study is expected to clarify their relationships undoubtedly.

The presence of *H. vervoorti*, originally described from the Caribbean (Galea, 2008), in the Indian Ocean is not entirely surprising. The reverse situation is, indeed, more common at present, with many examples of hydroids, primarily known to occur in the Indo-Pacific that were subsequently recorded from the Caribbean, *viz. Sertularia rugosissima* Thornely, 1904 (Galea, 2008), *S. tongensis* (Stechow, 1919) (Galea, 2010), *S. hattorii* Leloup, 1940 (Galea & Ferry, 2015), *Aglaophenia postdentata* Billard,

1913 (Galea, 2013), and *Clytia edentula* Gibbons & Ryland, 1989 (Galea & Ferry, 2015). Whether these species primarily occurred in one geographical area and spread afterwards elsewhere, could not be established at this stage, but it is obvious that only the frequency of the collecting efforts first revealed their presence in one area but not in the other.

Halopteris vervoorti comes close to a number of nominal species through the occurrence of paired axillar nematothecae behind the cauline hydrothecae and the heteromerous segmentation of its cladia, *viz*. *H. australis* sp. nov. (see below), *H. brasiliensis* (see below), *H. liechtensternii* (Marktanner-Turneretscher, 1890), and *H. sibogae* (Billard, 1913). However, unlike *H. australis*, it does not possess hydrothecae with distinctly sinuated margins or exceedingly-long lateral nematothecae, respectively. On the other hand, *H. brasiliensis* is a species forming taller cormoids, with thicker stems and cladia, broader hydrothecae, and cauline superior nematothecae distinctly arranged into two longitudinal rows; unlike in *H. vervoorti*, its cauline hydrothecae occupy nearly the whole length of the internode. *Halopteris liechtensternii* is a species with comparatively longer stem internodes (and, implicitly, more widely-spaced cladia), provided regularly with 2-3 superior nematothecae arranged in two distinct rows, its female gonothecae are much longer and almost cylindrical, while its males appear dwarfed compared to those of the present species. *Halopteris sibogae*, besides many common features shared with *H. vervoorti* (see under the former), is immediately distinguishable through its exceedingly long lateral nematothecae. Additional differences to other congeners are summarized in Appendix 1.

Distribution: Lesser Antilles (Galea, 2008, 2010, 2013), Cape Verde (Ansín Agís *et al*., 2001, as *H. polymorpha*), (?) Red Sea (Vervoort, 1967; as *Antennella secundaria*), Madagascar, the Maldives, Indonesia (present study), (?) Australia (Preker & Lawn, 2010, as *H. polymorpha*), (?) Japan [Hirohito (1974), as *Heterotheca buski* (*sic*!); Hirohito (1995), as *Halopteris buski* (*sic*!)], (?) Fiji (Ryland & Gibbons, 1991, as *Halopteris buskii*).

Halopteris australis Galea, sp. nov.

Figs 1E, 2F, 6; Table 5; Appendix 1

Halopteris buskii – Vervoort & Vasseur, 1977: 72, fig. 31 [non *Halopteris buskii* (Bale, 1884)].

Halopteris polymorpha – Schuchert, 1997 (*pro parte*): 64, fig. 23 [non *Halopteris polymorpha* (Billard, 1913)].

Type material: MHNG-INVE-82742; France, New Caledonia, Nouméa, south of N'Géa islet, -22.296° 166.489°, 9 m, coll. E. Tardy; 06.10.2012; fertile (female) colony in alcohol and two microslides (H20/37-38), with stems up to 1.8 cm high, growing on algae.

Diagnosis: Small-sized *Halopteris*, with cormoids not exceeding 2.5 cm high. Stems monosiphonic, homomerously-segmented, internodes rather long, bearing a hydrotheca in their proximal half, a lateral apophysis, and up to 8 nematothecae (1 mesial, a pair of laterals, a pair of axillar, as well as up to 3 superiors in two parallel rows). Cladia alternate, heteromerously-segmented; 1st ahydrothecate internode with 1, exceptionally 2, nematothecae in a row; ordinary ahydrothecate internodes with 1 nematotheca; hydrothecate internodes with a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and 1, or rarely 2, axillar); hydrotheca cup-shaped, deep, adnate for 2/3rd its adaxial wall, swollen basally, rim distinctly sinuated in lateral view, aperture circular, lateral nematothecae long, borne on well-developed apophyses, surpassing hydrothecal rim. Female gonothecae given off from caulus; piriform, borne on quadrangular pedicel, 2 basal nematothecae, aperture large, circular, perpendicular to long axis of theca, rim thickened, a watch-glass-shaped operculum.

Etymology: From the Latin *austrālis*, meaning "of the south" with reference to its occurrence in the South Pacific.

Description: Colonies composed of a varied number of upright cormoids, up to 2 cm high in present material, arising from creeping, branching, anastomosing hydrorhiza. Stems erect, simple, monosiphonic (Figs 1E, 2F), composed of a basal, ahydrothecate part, irregularly divided into a few segments (up to 5) by means of transverse constrictions of the perisarc, and carrying a varied number of nematothecae arranged in two parallel rows; above, remainder of stem comprising a much longer, hydrothecate part, homomerously-segmented into regular internodes by means of oblique nodes (Fig. 6A), slightly marked proximally to more conspicuous distally; occasionally, transverse nodes can be inserted towards the distal end of cauli, creating a heteromerous segmentation; a hinge joint between the two parts of the stem. Up to 26 relatively long cauline internodes, almost collinear proximally, gradually becoming geniculate towards distal end; each provided with a hydrotheca in its proximal half, a well-developed, lateral apophysis, as well as up to 8 nematothecae: 1 mesial, a pair of laterals, a pair of axillar (only one of these subsisting distally on stem) (Fig. 6B), as well as 1-3 superior ones in two parallel, closely-set rows (when only two of these are present, they may occur at the same level, or one above the other; they are confined to a separate ahydrothecate segment when transverse nodes intervene towards distal end of caulus). Cladia up to 2.5 mm long, alternate, except in the proximal most cauline internodes, where they are opposite; composed of a short, quadrangular segment proximally, followed by a heteromerous division into alternating ahydrothecate and hydrothecate internodes; the former

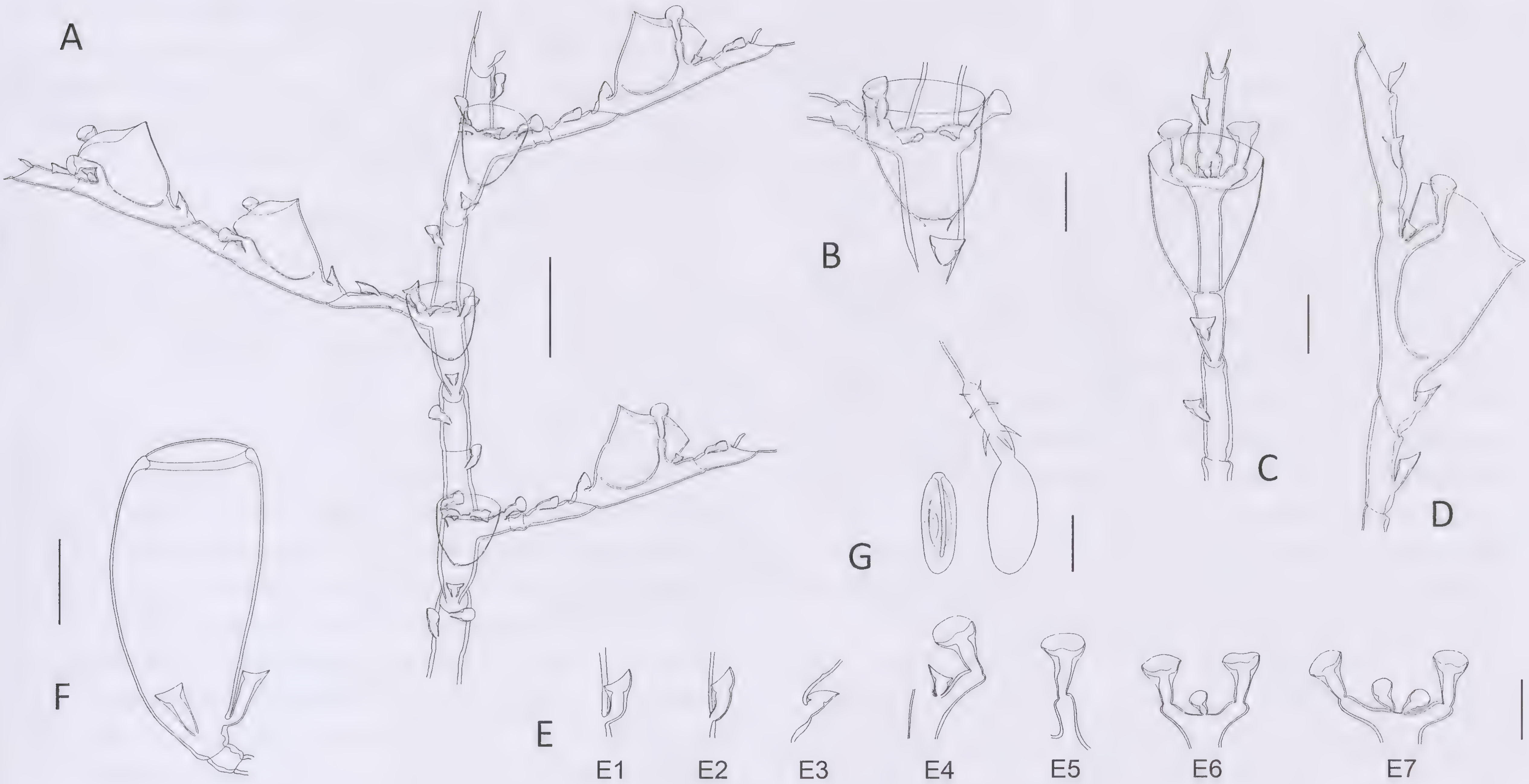

Fig. 6. *Halopteris australis* sp. nov. Portion of stem and basal parts of three cladia (A). Stem internode with hydrotheca (B). Portions of cladia enlarged in frontal (C) and lateral (D) aspects. Nematothecae (E): from caulus (E¹) and cladia (E²), mesial from cladial hydrotheca (E³), lateral from cauline (E⁴) and cladial (E⁵) hydrothecae, single (E⁶) and paired (E⁷) axillar associated to cladial hydrothecae. All from sample MHNG-INVE-82742. Scale bars: 10 µm (G), 100 µM (B-E), 200 µm (F), 300 µm (A).

with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes (Fig. 6D); 1st ahydrothecate internode comparatively longer than subsequent ones, and carrying single nematotheca (exceptionally 2); ordinary ahydrothecate internodes short, and provided with one nematotheca; hydrothecate internodes up to 5 per cladium, comparatively longer than their ahydrothecate counterparts, and carrying a centrally-placed hydrotheca and its up to 5 associated nematothecae: a mesial, a pair of laterals, and generally one axillar, although a pair could be occasionally noted (Fig. 6C). Hydrothecae cup-shaped, rather deep, about 1/3rd adnate; abaxial wall slightly sigmoid, rounded proximally and slightly flaring below the rim; aperture circular in apical view, but distinctly sigmoid when seen laterally, due to broad (though shallow) abaxial emargination, giving the impression that an abaxial cusps occurs (Fig. 6A, D). All nematothecae, including the axillar ones, bithalamic and movable; mesial nematothecae triangular in frontal view, with deep adaxial emargination (Fig. 6E³); laterals relatively long, surpassing the hydrothecal rim (Fig. 6D), and borne on well-developed apophyses; basal chamber high and narrow, upper chamber shallow, with sigmoid adaxial wall (Fig. 6E⁴⁻⁷); axillar nematothecae (Fig. 6E⁶˒⁷) small, with wall of upper chamber lowered on side facing adaxial wall of hydrotheca; both cladial (Fig. 6E²) and cauline (Fig. 6E¹) nematothecae characteristically turned posteriad, tall, conical, with rim of apical chamber lowered adaxially. Female gonothecae borne on cauli by means of short, lateral apophyses given off from below the hydrothecae, followed by a pedicel composed of a quadrangular segment; large, piriform, with 2 basal nematothecae, and a large, apical aperture with thickened rim, perpendicular to long axis of the theca, and closed by a watch-glass-shaped operculum (Fig. 6F). Male gonothecae elongated-ovoid, curved proximally and provided there with single nematotheca; aperture distal, small, circular. Hydranths badly preserved, tentacle number could not be ascertained. Cnidome (Fig. 6G): only large capsules (*ca.* 17.5 × 6.3 µm), likely pseudostenoteles, observed in the material in hand. Color in life: milky white (Fig. 1E).

Dimensions: See Table 5.

Remarks: There is little doubt that the present material from New Caledonia is conspecific with the specimens with distinctly sinuated hydrothecal margins from French Polynesia examined by Vervoort & Vasseur (1977, as *H. buskii*) and, subsequently, by Schuchert (1997, provisionally assigned to *H. polymorpha*). Their main morphological and morphometrical features are compared in Table 5. Unfortunately, it was not possible to obtain the material of Vervoort & Vassueur for a re-examination, due to ongoing renovation of NBC.

The cauline internodes bear commonly 1 (52%) or 2 (44%) superior nematothecae, although up to 3 may occasionally (4%, n = 75 internodes belonging to 5

different stems) be present in the material in hand. Schuchert (1997), however, reports up to 5 of these. The number of axillar nematothecae was apparently overlooked by Vervoort & Vasseur (1977):

1) Schuchert (1997) stated that, occasionally, these may occur in pairs behind the hydrocladial hydrothecae, a conclusion confirmed by our observations;
2) it was noted that, on cauli, one nematotheca of a pair, namely that bent towards the cladium, is hidden by the apophysis supporting its lateral counterpart, and requires a careful examination to be noticed; alternatively, it should be stated that only one nematotheca of a pair subsists on the distalmost cauline internodes.

Only female gonothecae occur in the present material (Fig. 6F), although those of both sexes were illustrated by Schuchert (1997, fig. 23B, right).

Halopteris australis, through the presence of pairs of axillar nematothecae especially on the stem, and the heteromerous segmentation of its cladia, resembles *H. brasiliensis* sp. nov., *H. liechtensternii*, and *H. vervoorti*. However, any of these is provided with the distinctively sinuated hydrothecal margin displayed by it. In addition, *H. brasiliensis* has thicker stems and cladia, its lateral nematothecae are relatively short and conical, and do not surpass the hydrothecal rim. *Halopteris liechtensternii* is readily distinguished through the shape and size of its gonothecae, the females being long and almost tubular, while the males are dwarfed. *Halopteris vervoorti* forms comparatively shorter cormoids, with shorter stem internodes (and, consequently, more approximated cladia) provided with 1-2 superior nematothecae characteristically arranged in a row, and its hydrothecae are slightly shorter and narrower. Additional differences to other congeners are summarized in Appendix 1.

Distribution: New Caledonia (present study), French Polynesia (Vervoort & Vasseur, 1977; as *H. buskii*).

Halopteris millardae Galea, sp. nov.

Figs 1F, 2G, 7; Table 5; Appendix 1

Halopteris polymorpha – Millard & Bouillon, 1973 (*pro parte*): 83, fig. 10F, G, H, J. – Bouillon *et al*., 1995: 49. – Schuchert, 1997 (*pro parte*): 66, 72, fig. 22A-D [non *Halopteris polymorpha* (Billard, 1913)].
non *Halopteris polymorpha* – Millard & Bouillon, 1973 (*pro parte*): 83 (= *H. platygonotheca* Schuchert, 1997).
Halopteris buskii – Rees & Vervoort, 1987 (*pro parte*): 119, fig. 25A-B [non *Halopteris buskii* (Bale, 1884)].

Holotype material: MACT2700; Seychelles, Mahé I., coll. J. Bouillon (MRAC Expedition); 1966; numerous cormoids, 1.5-7 cm high, with both female and male gonothecae [material studied by Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913); not studied here due to ongoing renovation of MRAC; however, 4 microslides (MHNG-INVE-37494, H12/32-35) prepared from the holotype, were examined for the purpose of the present study; according to Schuchert (1997: 55), cormoids of *H. platygonotheca* Schuchert, 1997 co-occur in the original sample].

Paratype: MHNG-INVE-98634; Republic of Maldives, Faafu Atoll, 3.06497° 72.9212°, 35 m, coll. D. Maggioni and S. Montano; 14.04.2016; colony composed of 6 sterile stems, 1.7-3.9 cm high; 16S sequence MF773747.

Diagnosis: *Halopteris* with tall cormoids, reportedly reaching 7 cm high; stems homomerously-segmented, each internode moderately-long, carrying a hydrotheca, a lateral apophysis, and up to 7 nematothecae: 1 mesial, a pair of laterals, a scale-shaped axillar one, as well as 2-3 superior ones arranged in two parallel rows; cladia alternate, heteromerously-segmented; ahydrothecate internodes with 2 laterally-displaced nematothecae (distally, only 1 of these subsists); hydrothecate internodes with a hydrotheca and its 4 associated nematothecae: 1 mesial, a pair of laterals, and a small, scale-shaped axillar one. Colonies monoecious. Female gonotheca borne on stems, large, ovoid, laterally flattened, with 2 basal nematothecae, and a distal, transverse aperture closed by glass-watch-shaped operculum. Male gonothecae borne on both stems and cladia, small, fusiform, with narrow distal aperture, and one basal nematotheca.

Etymology: This species honors the late N.A.H. Millard (1914-1997) for her outstanding contribution to the hydrozoan research.

Description: Colonies composed of a varied number of tall stems (reportedly up to 7 cm in height) arising from tortuous, creeping, branching, anastomosing hydrorhiza, devoid of nematothecae. Stems erect, simple, monosiphonic (Figs 1F, 2G), composed of a basal, ahydrothecate part of varied length, and a much longer, distal part bearing hydrothecae and hydrocladia; basal part arising directly from hydrorhiza without constriction above origin, usually not segmented by transverse nodes, and carrying a varied number of nematothecae in two parallel rows; distalmost node deeply-cut and oblique; remainder of stem homomerously-segmented into regular internodes by means of oblique nodes; each internode moderately long, with a hydrotheca in its basal half, a short lateral apophysis supporting a cladium, and up to 8 nematothecae: 1 mesial, a pair of laterals, a small, scale-shaped axillar one, as well as generally 2, occasionally 3, or exceptionally 4, superior nematothecae arranged in two parallel rows (Fig. 7A, B); proximal most internode carries 2 opposite apophyses supporting a pair of cladia, and usually bears 3-4 superior nematothecae. Cladia borne on corresponding stem apophyses, alternate, composed of a proximal, short, quadrangular segment, followed by a succession

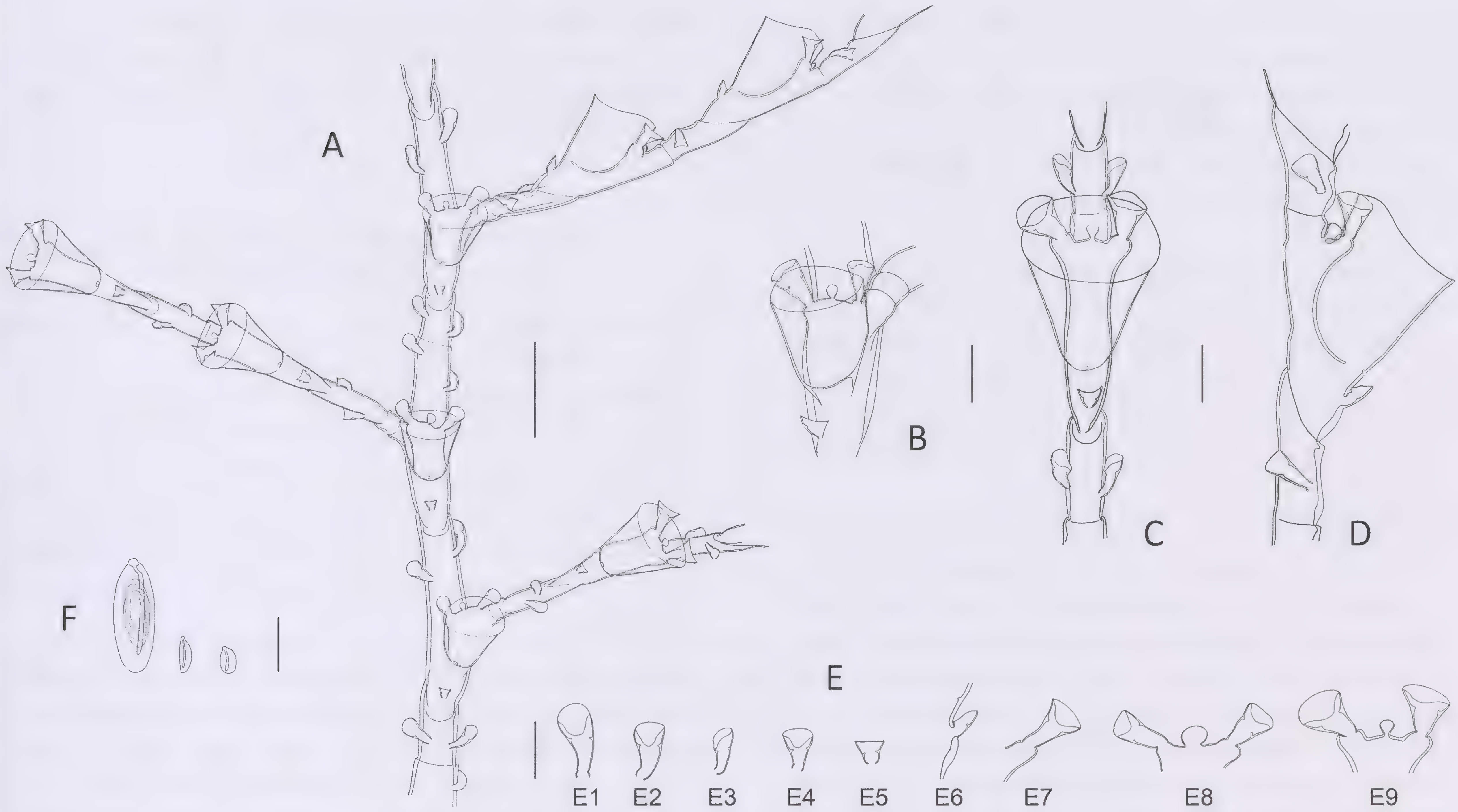

Fig. 7. *Halopteris millardae* sp. nov. Portion of stem with basal parts of three cladia (A). Hydrothecae from stem (B) and cladia (C, D), the latter in frontal and lateral aspects, respectively. Nematothecae (E): from caulus ($E^{1,2}$) and ahydrothecate cladial internodes ($E^{3,4}$), mesial ($E^{5,6}$) and lateral (E^{7}) from cauline hydrotheca, and axillar associated to both cauline (E^{8}) and cladial (E^{9}) hydrothecae. All from sample MHNG-INVE-98634. Scale bars: 10 μm (F), 100 μm (B-E), 300 μm (A).

of athecate and thecate internodes resulting from a heteromerous segmentation (Fig. 7A); ahydrothecate internodes with straight node proximally and oblique node distally; the reverse in hydrothecate internodes; the latter, up to 5 per cladium in the material in hand, comprising a centrally-placed hydrotheca, and its 4 associated nematothecae: 1 mesial, a pair of laterals, as well as a minute, scale-shaped axillar one (Fig. 7C, D); ahydrothecate internodes shorter than their hydrothecate counterparts, with generally 2 laterally-displaced nematothecae, either opposite or subopposite, more often found in proximal most internodes, whereas only one of these is retained by the distalmost internodes. Hydrothecae cup-shaped, moderately-deep, fused for about 1/3rd their adaxial length; abaxial wall straight for most of its length, slightly everted below aperture; the latter perfectly circular in apical view, slightly flaring and showing a sinuated rim in lateral view, though not producing an abaxial cusp (Fig. 7D). All nematothecae, except the axillar ones, bithalamic and movable; mesial ones triangular in frontal view, with deeply-scooped rim on adaxial side (Fig. 7$E^{5,6}$); laterals borne on rather short apophyses, conical, with thickened walls (Fig. 7E^{7}), not surpassing the hydrothecal rim (Fig. 7D); cauline (Fig. 7$E^{1,2}$) and cladial (Fig. 7$E^{3,4}$) nematothecae characteristically turned posteriad (Fig. 7A, C), long, conical, with tall basal chambers and comparatively shallow apical chambers, with adaxially-scooped rims; axillar nematothecae associated to the hydrothecae of both caulus (Fig. 7E^{8}) and cladia (Fig. 7E^{9}), monothalamic. Stems monoecious. Female gonothecae borne below the stem hydrothecae through short lateral apophyses and a single-segmented, quadrangular pedicel; large, ovoid, laterally-flattened, with two nematothecae on base, and a distal, transverse, conspicuously thickened aperture closed by a glass-watch-shaped operculum. Male gonothecae borne on both stems and cladia, through short, lateral apophyses and a single-segmented, quadrangular pedicel; comparatively smaller than female, fusiform, with distal, narrow, circular aperture, and a basal nematotheca. Color in life: brownish (Fig. 1F). Cnidome (Fig. 7F) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(19.9-21.3) × (7.3-8.0) μm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(5.8-6.5) × (2.1-2.3) μm, in tentacles]; small, ovoid capsules [(5.1-5.8) × (2.9-3.1) μm, scattered in the coenosarc].

Dimensions: See Table 5.

Remarks: Upon comparison of the newly-collected Maldivian specimens with the slide material MHNG-INVE-37494 (H12/32-35) prepared from the holotype designated herein [sample MACT2700 studied by

Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913)], it appears that both are conspecific.

The description of the gonothecae, often distorted in the slide material available (H12/32: ♂; H12/33: ♂ & ♀; H12/35: ♂), was taken after Millard & Bouillon (1973: 84, fig. 10H & J) and Schuchert (1997: 22, fig. 22D, as *H. polymorpha*).

The tallest cormoid examined here (3.9 cm high) bears 54 cauline hydrothecate internodes. Not only the proximal most internode gives rise to a pair of cladia, but this situation is also repeated in several subsequent, consecutive, more distal internodes. In one cormoid, a secondary stem arises from one of the paired, basalmost hydrocladia.

The first cladial ahydrothecate internodes do not differ much in length compared to their subsequent counterparts; they generally bear 2 nematothecae, though exceptionally 3 were noted. The remaining internodes equally bear 2 nematothecae (although, exceptionally, two pairs could be found) when they are found in the proximal parts of the cladia, while only one nematotheca occurs in those internodes confined to the distalmost parts of the cladia.

Rees & Vervoort's (1987) record from Zanzibar (Stn. 112) assigned to *H. buskii* likely belongs to the present species. Indeed, the occurrence of pairs of suprahydrothecal nematothecae, and of a single axillar nematotheca on the cauline internodes, are distinctive. However, the authors mention only one nematotheca per ahydrothecate cladial internode; as stated above, this situation is, quite often, met with in the distalmost internodes of the material MHNG-INVE-37494. It should also be stressed that only one nematotheca of a couple is visible when the cladia are seen laterally, especially in material mounted between slide and coverslip. Strangely, Rees & Vervoort do not mention a sinuated hydrothecal rim, though it should be underlined that this peculiarity is only noticeable towards the adaxial thecal wall, where the presence of lateral nematothecae could make it less obvious upon a routine examination.

Halopteris millardae comes close to a few congeners with homomerously-segmented cauli and a heteromerous division of their cladia, and whose both cauline and cladial hydrothecae are provided with an axillar nematotheca, namely *H. nuttingi* (Billard, 1911) and *H. polymorpha*. *Halopteris nuttingi* has proportionally shorter cauline internodes [compare fig. 21B in Schuchert (1997) with Fig. 7A herein], provided with up to three pairs of superior nematothecae in two parallel rows, and the upper chamber of its lateral nematothecae is globular, with the rim scooped on both ad- and abaxial walls [Billard (1913), as *H. buski* (*sic!*); Schuchert (1997, fig. 21C, H), as *H. polymorpha*]. *Halopteris polymorpha* has comparatively longer stem and cladial ahydrothecate internodes (Fig. 3A, B), its hydrothecae are shallower (Fig. 3D, F) and are provided with an even rim. Additional differences to other congeners are summarized in Appendix 1.

Distribution: Seychelles [Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913)], Maldives (present study), Zanzibar [Rees & Vervoort (1987), as *H. buskii* (Bale, 1884)].

Halopteris brasiliensis Galea, sp. nov.

Figs 2H, 8; Table 5; Appendix 1

Halopteris buskii. – Migotto, 1996: 48, fig. 9F-H [non *Halopteris buskii* (Bale, 1884)].

Halopteris polymorpha. – Schuchert, 1997 (*pro parte*): 72, fig. 22F-H [non *Halopteris polymorpha* (Billard, 1913)].

Holotype material: MHNG-INVE-37495; Brazil, São Sebastião Channel, 6-8 m, coll. A.E. Migotto; 06.10.1987; two slides, H12/36 & 37, each containing a *ca.* 1.6 cm high cormoid provided with a female gonotheca.

Diagnosis: *Halopteris* with medium-sized plumes, reaching 3 cm high; stems simple, monosiphonic, homomerously-segmented; internodes rather short, with a lateral apophysis, a hydrotheca, and its up to 7 associated nematothecae (1 mesial, a pair of laterals, a pair of axillar, and generally 2 superiors, the latter either opposite or subopposite). Hydrocladia alternate, heteromerously-segmented; ahydrothecate internodes very short, with 1 nematotheca; hydrothecate internodes comparatively longer, with one hydrotheca and up to 5 nematothecae (1 mesial, a pair of laterals, and commonly 1, rarely 2, axillar). Female gonothecae borne on stems; large, piriform, with 2-3 long, basal nematothecae, aperture distal, wide, circular, perpendicular to long axis of theca, closed by glass-watch-shaped operculum.

Etymology: Named after the country of occurrence.

Description: Colonies composed of reportedly up to 3 cm high cormoids arising from creeping, branching hydrorhiza. Stems erect, simple, monosiphonic (Fig. 2H), composed of a basal, ahydrothecate portion, and a much longer, distal part bearing both hydrothecae and hydrocladia. The former of varied length, irregularly divided into a number of segments by means of transverse nodes, bearing nematothecae arranged in two longitudinal rows; last node deeply-cut and oblique. Remainder of caulus homomerously-segmented into rather short internodes by means of oblique nodes (Fig. 8A); each internode with a hydrotheca in its proximal half, a cladial apophysis lateral to it (two opposite in proximal most internode), and up to 7 nematothecae, of which 5 are associated to the hydrotheca (1 mesial, a pair of laterals, and a pair of axillar) (Fig. 8B), and 2 (slightly displaced laterally and, thus, forming an opposite or a subopposite pair) occur distally on the internode (occasionally, only one of these is present; however, in the basalmost internodes bearing pairs of cladia, 2-3 of these occur). Hydrocladia

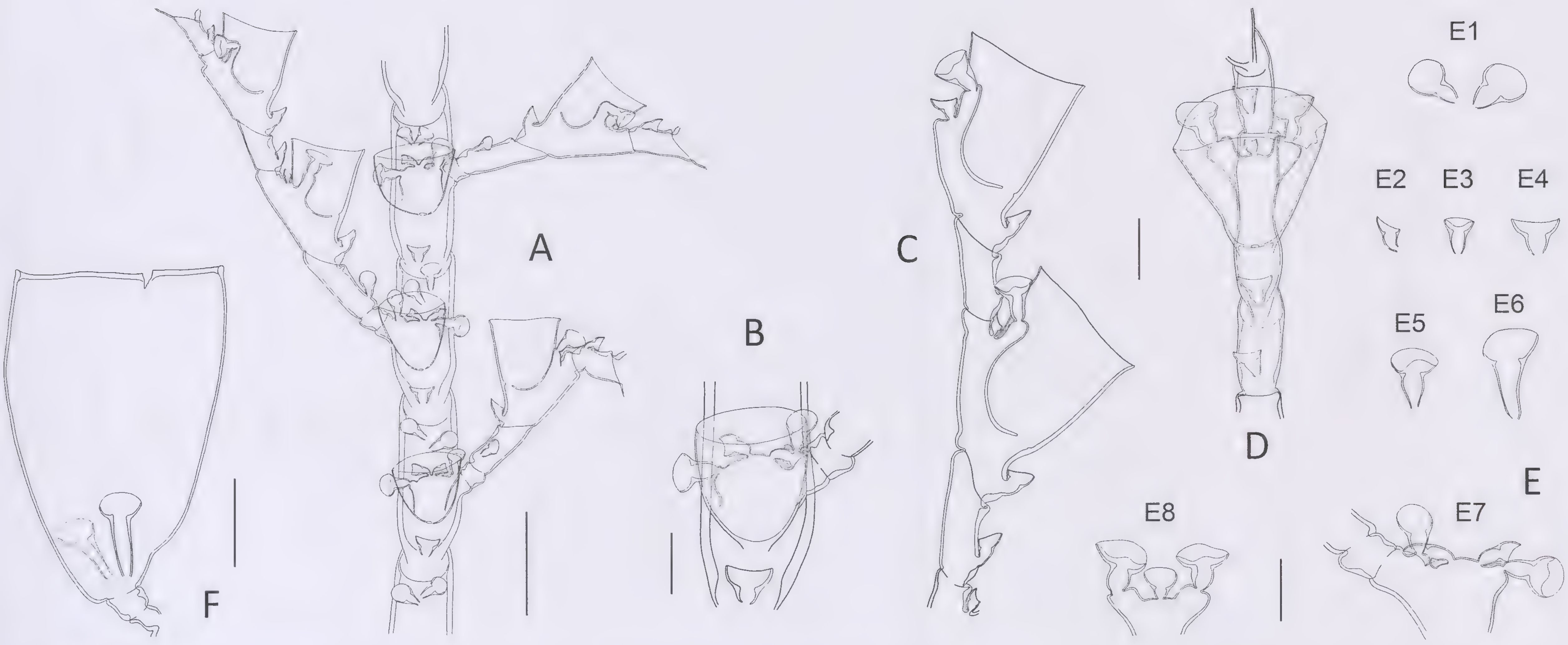

Fig. 8. *Halopteris brasiliensis* sp. nov. Portion of stem with basal parts of three cladia (A). Stem hydrotheca (B). Portions of cladia in lateral (C) and frontal (D) aspects. Nematothecae (E): from caulus (E^1) and ahydrothecate cladial internodes ($E^{2,3}$), mesial from cauline hydrotheca (E^4), lateral from cladial hydrotheca (E^5), from female gonotheca (E^6), pair of axillar from cauline hydrotheca (E^7) and single axillar from cladial hydrotheca (E^8). All from sample MHNG-INVE-37495. Scale bars: 100 µm (B-E), 200 µm (F), 300 µm (A).

alternate, borne on corresponding cauline apophyses; composed of a short, athecate, quadrangular segment, followed by an alternation of ahydrothecate and hydrothecate internodes resulting from a heteromerous segmentation (Fig. 8C); ahydrothecate internodes with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes; first ahydrothecate internode comparatively longer than subsequent ones, and carrying a single nematotheca; ordinary ahydrothecate internodes very short and provided with single nematotheca; hydrothecate internodes, reportedly up to 7 per hydrocladium, accommodating a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and commonly one – rarely a pair – of axillar nematothecae) (Fig. 8D). Hydrothecae cup-shaped, rather deep, adnate for about half their height, walls slightly divergent, abaxial one imperceptibly sigmoid (concave proximally, convex below aperture), free part of adaxial one straight; aperture wide, circular, rim even (Fig. 8C). Hydranths with conical hypostome and 16-17 filiform tentacles. All nematothecae, including the axillar ones, bithalamic and movable; mesial ones short, with lower and upper chambers of nearly same depth (Fig. 8E^4), and rim of upper chamber lowered on adaxial side; lateral nematothecae borne on well-developed apophyses, with tall basal chamber and shallow upper chamber with sigmoid rim on adaxial side (Fig. 8E^5); whole nematotheca barely reaching hydrothecal rim (Fig. 8C); cauline (Fig. 8E^1) and cladial (Fig. 8$E^{2,3}$) nematothecae similar in shape to the laterals, but with lowered rim on the adaxial side of upper chamber; cauline axillar nematothecae displaced laterally and facing outwards in opposite directions (Fig. 8E^7); cladial axillar nematothecae commonly occurring singly (Fig. 8E^8), reportedly in pairs in rare instances. Gonothecae (only female known) borne on both cauli and cladia, given off laterally from below the hydrothecal bases; large, piriform, with 2-3 long, basal nematothecae, and a broad, circular aperture with thickened rim, perpendicular to long axis of the theca (Fig. 8F), and closed by glass-watch-shaped operculum. In life, coenosarc yellowish, hydranths white. Cnidome: at least pseudostenoteles [(18.0-21.5) × (7.5-9.0) µm] and microbasic mastigophores [(6.0-7.0) × *ca.* 2.0 µm] reported to date.

Dimensions: See Table 5.

Remarks: The description given above is based on the holotype, although some additional data, such as the cnidome composition, are taken from Migotto (1996, as *H. buskii*).

Through the presence of pairs of cauline axillar nematothecae and the heteromerous segmentation of its cladia, *H. brasiliensis* comes close to a number of congeners, *viz. H. australis* sp. nov., *H. liechtensternii*, *H. sibogae*, and *H. vervoorti*. *Halopteris australis* is immediately distinguished through it distinctly sinuated hydrothecal margin. *Halopteris liechtensternii,* when fertile, has comparatively longer and more tubular female gonothecae. *Halopteris sibogae* has distinctive, exceedingly long nematothecae (Fig. 2C). *Halopteris vervoorti* forms comparatively shorter stems (compare Fig. 2C-E and 2H), their cauli and cladia are thinner (compare Fig. 5A, B, M and 8A), and their cauline hydrothecae are placed in the lower halves of the corresponding internodes, leaving enough place for

Table 1. Comparative morphological and morphometrical features of *H. polymorpha* (Billard, 1913) (present study and syntype materials from *Siboga* Stn. 80 and 299) and *H. sibogae* (Billard, 1913) (Ho stands for homomerous, and He for heteromerous).

	***Halopteris polymorpha* (Billard, 1913)**			***Halopteris* sp.**	***Halopteris sibogae* (Billard, 1913)**	
	Present study, MHNG-INVE-97937	Billard (1913), *Siboga* Stn. 80	Schuchert (1997), *Siboga* Stn. 80	Present study, MNHN H.L. 1309, *Siboga* Stn. 299	Present study, MHNG-INVE-97926	Billard (1913), as *H. polymorpha* var. *sibogae*
Caulus (seen frontally)						
- segmentation	Ho	-	Ho	Ho (distally He)	Ho	-
- superior nematothecae / internode with opposite cladia	4-5	-	-	-	3-4	-
- nematothecae above hydrotheca in ordinary internodes	Commonly 2-3 (range 1-5)	-	2 (rarely 1 or 3)	2	2-3	-
- number of axillar nematothecae	1	1	1	2	1-2	-
- internode length	695-955	-	-	515-570	450-605	-
- diameter at node	145-230	-	-	115-130	90-125	-
- length of apophysis	70-80	-	-	-	70-80	-
- length of nematothecae	80-100	-	-	65-70	100-125	-
- diameter of nematothecae at rim	55-65	-	-	35-45	45-50	-
Cladia (seen laterally)						
- segmentation	He	He	He	He	He	He
- nematothecae on 1st ahydrothecate internode	2	2	2	2 (occ. 3)	2	
- nematothecae on ordinary ahydrothecate internodes	1-2	Commonly 2	2	1-2	1-2	1
- number of axillar nematothecae	0-1	1	1	1	1-2	-
- length of quadrangular segment	65-80	-	-	45-60	40-45	-
- length of 1st ahydrothecate internode	475-730	580-700	-	220-310	270-365	200-240
- length of ordinary ahydrothecate internodes	315-460	380-470	340-400	160-300	180-270	135-190
- length of hydrothecate internodes	350-395	340-380	320	255-330	285-350	270-380
- diameter at transverse node	65-80	-	-	35-45	40-50	55-60
- length of nematothecae	55-80	-	-	40-60	55-110	-
- diameter at rim of nematotheca	35-50	-	-	35-40	35-50	-
Hydrotheca (cladial)						
- length abaxial wall	145-165	135-160	150-160	200-235	200-215	190-215
- length free adaxial wall	90-110	-	80-90	110-125	100-110	-
- diameter at rim	220-245	200-215	200-210	160-200	160-180	190-200

	***Halopteris polymorpha* (Billard, 1913)**			***Halopteris* sp.**	***Halopteris sibogae* (Billard, 1913)**	
	Present study, MHNG-INVE-97937	Billard (1913), *Siboga* Stn. 80	Schuchert (1997), *Siboga* Stn. 80	Present study, MNHN H.L. 1309, *Siboga* Stn. 299	Present study, MHNG-INVE-97926	Billard (1913), as *H. polymorpha* var. *sibogae*
- length apophyses of lateral nematothecae	40-55	-	-	50-60	95-105	-
- length lateral nematotheca	70-80	-	-	80-90	125-145	-
- diameter of lateral nematotheca at rim	65-80	-	-	50-60	55-65	-
- length of mesial nematotheca	60-65	-	-	45-55	55-60	-
- diameter at rim of mesial nematotheca	45-50	-	-	40-45	45-50	-
- length of axillar nematotheca	*ca.* 40	-	-	30-35	40-55	-
- diameter of axillar nematotheca at rim	*ca.* 35	-	-	*ca.* 20	30-40	-
Gonotheca						
- length of pedicel	70-80 (♂); *ca.* 80 (♀)	-; -	-; -	-; -	30-45 (♂); *ca.* 45 (♀)	-; -
- length (excluding pedicel)	490-560 (♂); 1015-1040 (♀)	-; -	- (♂); *ca.* 650 (♀)	-; -	330-440 (♂); 620-685 (♀)	-; -
- maximum width	210-240 (♂); 480-510 (♀)	-; -	-; -	-; -	165-220 (♂); 310-365 (♀)	-; -
- diameter at aperture (♀)	330-350	-	-	-	180-215	-
- number of basal nematothecae	2 (♂); 2-3 (♀)	- (♂); 3 (♀)	- (♂); 2-3 (♀)	-; -	2 (♂); 3 (♀)	-; -

Table 2. Literature records included earlier in the synonymy of *Halopteris polymorpha* (Billard, 1913), but deviating from the present concept of this species (*H.* stands for *Halopteris*). N.B.: Italics are used to emphasize the distinguishing characters.

Original assignation	Reference	Geographical origin	Morphological features not agreeing with *H. polymorpha*	Possible correct taxonomical status
***Plumularia nuttingi* Billard, 1911**	Billard (1911)	Indonesia	Cauline internodes with *1 axillar* and *1-2 pairs of superior nematothecae*; cladia homo- to heteromerously-segmented; hydrothecate internodes with 1 axillar nematotheca; ahydrothecate internodes with 1-2 nematothecae; upper chamber of lateral nematothecae *globular, with distinctly emarginated ad- and abaxial walls*	*H. nuttingi* (Billard, 1911)
***Plumularia buskii* Bale, 1884**	Thornely (1904)	Sri Lanka	Neither described, nor illustrated	Unidentifiable
	Ritchie (1910)	Christmas I.	Description incomplete, partly illustrated subsequently by Vervoort & Vasseur (1977, fig. 30C)	Unidentifiable
	Thornely (1916)	India	Neither described, nor illustrated	Unidentifiable
	Nutting (1927)	Philippines	No formal description, no illustration	Unidentifiable

Original assignation	Reference	Geographical origin	Morphological features not agreeing with *H. polymorpha*	Possible correct taxonomical status
***Plumularia buski (sic!)* Bale, 1884**	Hartlaub (1901)	Hawai'i	No formal description, illustrations insufficient	Unidentifiable
	Billard (1913)	Indonesia	Cauline internodes with *1 axillar* and *1-3 pairs of superior nematothecae*; cladia homo- to heteromerously-segmented; hydrothecate internodes with 1 axillar nematotheca; ahydrothecate internodes with 1-2 nematothecae; upper chamber of lateral nematothecae *globular, with distinctly emarginated ad- and abaxial walls*	*H. nuttingi* (Billard, 1911)
	Redier (1966)	New Caledonia	No formal description, but *homomerous* segmentation of the cladia, and lateral nematothecae with *globular upper chamber*	*H. nuttingi* (Billard, 1911)
***Halopteris buskii* (Bale, 1884)**	Vervoort & Vasseur (1977)	Fr. Polynesia	Hydrotheca with distinctly *sinuated margin*, tall lateral nematothecae	*H. australis* sp. nov.
	Rees & Vervoort (1987)	Zanzibar	Relatively tall stems; cauline internodes with *unpaired axillar* nematotheca and *2 laterally-displaced* nematothecae above hydrotheca	*H. millardae* sp. nov.
	Ryland & Gibbons (1991)	Fiji	Cauline internodes with *2 axillar* nematothecae and *1-3 superiors*; cladia *heteromerously*-segmented, ahydrothecate internodes *shorter* than hydrothecate counterparts and with *1 nematotheca*, hydrothecate internodes with *1-2 axillar* nematothecae	Presumably *H. vervoorti* Galea, 2008
	Migotto (1996)	Brazil	Cauline internodes with *2 axillar* nematothecae and *1-2 superiors displaced laterally*; cladia heteromerously-segmented, ahydrothecate internodes with 1 nematotheca, hydrothecate internodes with 1-2 axillar nematothecae	*H. brasiliensis* sp. nov.
	Preker (2001, 2005)	Australia	Neither described, nor illustrated	Unidentifiable
***Halopteris buski* (Bale, 1884) (*sic!*)**	Hirohito (1974)	Japan	Neither described, nor illustrated	Unidentifiable
	Hirohito (1995)	Japan	Cauline internodes with *2 axillar* and *1-2 superior nematothecae*; cladia *heteromerously*-segmented, ahydrothecate internodes *shorter* that hydrothecate counterparts and with *1 nematotheca*, hydrothecate internodes with *1-2 axillar nematothecae*	Presumably *H. vervoorti* Galea, 2008
***Heterotheca buski* (Bale, 1884) (*sic!*)**	Hirohito (1974)	Japan	Cauline internodes with *2 axillar* nematothecae and *1, exceptionally 2, superiors*; cladia *heteromerously*-segmented; ahydrothecate internodes *shorter* than hydrothecate counterparts and with *1 nematotheca*; hydrothecate internodes with *1, exceptionally 2, axillar* nematothecae	Presumably *H. vervoorti* Galea, 2008
***Antennella polymorpha* (Billard, 1913)**	Vervoort (1941)	Philippines	No formal description, no illustration, possibly a mix of species	Unidentifiable in the absence of a reexamination
***Halopteris polymorpha* (Billard, 1913)**	Pennycuik (1959)	Australia	Material reportedly agreeing "closely with Billard's figure XIVA", though neither described, nor illustrated	Questionably *H. polymorpha* (Billard, 1913)
	Vervoort (1966)	South Africa	Stems internodes with single axillar nematotheca and 1 median superior nematotheca, cladia *homomerously*-segmented, internodes with single axillar and median superior nematotheca	Related to *H. vervoorti* Galea, 2008, but of larger proportions; unidentifiable
	Millard & Bouillon (1973)	Seychelles	Mix of species (Schuchert, 1997)	*H. millardae* sp. nov. + *H. platygonotheca* Schuchert, 1997
	Millard & Bouillon (1974)	Mozambique	Small-sized cormoids, neither described, nor illustrated	Uncertain in the absence of a reexamination
	Millard (1975)	South Africa	Likely a mix of species: one with deep, cylindrical hydrothecae (fig. 112K), the other with shallow and conical hydrothecae (fig. 112L)	Unidentifiable species + (?) *H. buskii* (Bale, 1884), respectively
	Millard (1977)	South Africa	Neither described, nor illustrated	Uncertain in the absence of a reexamination
	Millard (1980)	South Africa	Neither described, nor illustrated	Uncertain in the absence of a reexamination

Original assignation	Reference	Geographical origin	Morphological features not agreeing with *H. polymorpha*	Possible correct taxonomical status
	Hirohito (1983)	Japan	Stem internodes with 2 axillar and *1-2 laterally-displaced* superior nematothecae; cladia *homomerously*-segmented, internodes with 1-2 axillar and 1 median superior nematothecae; hydrothecae *large*	Unidentifiable
	Ryland & Gibbons (1991)	Fiji	*Long* cauline and cladial hydrothecate internodes, *shallow* hydrothecae, *short* apophyses supporting the lateral nematothecae, single axillar nematothecae	*H. polymorpha* (Billard, 1913)
	Bouillon *et al.* (1995)	Seychelles	No description or illustrations available	Presumably *H. millardae* sp. nov.
	Schuchert (1997)	Various localities	Mix of species	*H.* sp. (fig 20B), *H. nuttingi* (Billard, 1911) (fig. 21), *H. millardae* sp. nov. (fig. 22A-D), *H. sibogae* (Billard, 1913) (fig. 22E), *H. brasiliensis* sp. nov. (fig. 22F-H), *H. australis* sp. nov. (fig. 23).
	Watson (2000)	Australia	Likely 2 species involved, one with comparatively deeper hydrothecae and flared lateral nematothecae (35D), the other shallow hydrothecae and lateral nematothecae with globular upper chamber (fig. 35C); description incomplete, some illustrations either misleading (*e.g.* fig. 35B, number of axillar and superior nematothecae unclear) or providing insufficient details (*e.g.* fig. 35A, number of cauline nematothecae impossible to ascertain)	Possibly *H. vervoorti* Galea, 2008 + unidentifiable species, respectively
	Ansín Agís *et al.* (2001)	Cape Verde	See Galea (2008)	Presumably *H. vervoorti* Galea, 2008
	Preker (2001, 2005)	Australia	Neither described, nor illustrated	Unidentifiable
	Kirkendale & Calder (2003)	Guam	Neither described, nor illustrated, but cormoids reportedly said "translucent-white", thus different from the distinctive yellow ones of *H. polymorpha*	Unidentifiable
	Preker & Lawn (2005)	Australia	Neither described, nor illustrated	Unidentifiable
	Ansín Agís *et al.* (2009)	Coral Sea	Neither formally described, nor illustrated	Unidentifiable
	Preker & Lawn (2010)	Australia	Stem internodes with 1 axillar nematotheca and *2 superiors*; cladia heteromerously-segmented, ahydrothecate internodes *shorter* that hydrothecate counterparts, and bearing 1 (rarely 2) nematothecae; hydrothecate internodes with *1 axillar* nematotheca	Presumably *H. vervoorti* Galea, 2008.
	Preker & Lawn (2012)	Australia	Single cauline axillar nematothecae, and 1-2 superiors; cladia heteromerously-segmented, ahydrothecate internodes *longer* than hydrothecate counterparts and bearing *1-2 nematothecae*, hydrothecate internodes with single axillar nematotheca	Unidentifiable
***Plumularia polymorpha* Billard, 1913**	Billard (1913)	Indonesia	According to the description, illustrations, and measurements, likely three species are involved	*H. polymorpha* (Siboga Stn. 80), *H* sp. (Stn. 77), and *H.* sp. (Stn. 299)
***Antennella secundaria* (Gmelin, 1791)**	Vervoort (1967)	Red Sea	Stem internodes with 1 axillar nematotheca and *"(usually) a distal"* nematotheca. Cladia heteromerously-segmented, ahydrothecate internodes comparatively *shorter* than hydrothecate counterparts and with *1 nematotheca*, hydrothecate internodes with *single axillar* nematotheca	Presumably *H. vervoorti* Galea, 2008

Table 3. Comparative measurements (in µm) and main morphological features of *H. vervoorti* Galea, 2008 from various localities. Ho stands for homomerous and He for heteromerous.

Geographical origin	Bali	Madagascar	Maldives	Guadeloupe, Martinique (*)
Reference(s)	Present study	Present study	Present study	Galea (2008); present study (*)
Caulus (seen frontally)				
- maximum height (cm)	1.2	0.8	1.3	2
- segmentation	Ho (dist. He)	Ho (dist. He)	Ho (dist. He)	Ho (dist. He)
- superior nematothecae / internode with opposite cladia	2	1-2	1-2	1-2 (*)
- nematothecae above hydrotheca in ordinary internodes	1-2, in a median row	1-2, in a median row	1-2, in a median row	1-2, in a median row
- number of axillar nematothecae	2 (distally 1)	2 (distally 1)	2 (distally 1)	2 (distally 1) (*)
- internode length	380-445	410-490	360-500	330-465
- diameter at node	55-110	45-105	60-115	-
- length of apophysis	65-80	85-95	60-75	60-70
- length of nematothecae	55-75	65-70	65-80	-
- diameter of nematothecae at rim	45-50	35-45	40-45	-
Cladia (seen laterally)				
- segmentation	He	He	He (occ. Ho)	He
- number of nematothecae on 1st ahydrothecate internode	1	1	1 (occ. 2)	1 (occ. 2) (*)
- nematothecae on ordinary ahydrothecate internodes	1	1	1	1
- number of axillar nematothecae	1 (rarely 2)	1 (rarely 2)	1 (rarely 2)	1 (rarely 2)
- length of quadrangular segment	45-50	50-60	40-55	70-90
- length of 1st ahydrothecate internode	190-270	160-240	175-255	155-215
- length of ordinary ahydrothecate internodes	125-160	160-205	140-190	115-170
- length of hydrothecate internodes	245-330	255-315	270-315	251-300
- diameter at transverse node	35-40	40-45	40-45	-
- length of nematothecae	50-70	55-65	55-70	-
- diameter at rim of nematotheca	35-40	35-40	30-45	-
Hydrotheca (cladial)				
- shape of the rim (lateral view)	Even	Even	Even	Even
- length abaxial wall	180-215	180-205	180-215	220-245
- length free adaxial wall	110-115	110-120	110-120	115-135
- diameter at rim	155-175	180-190	165-175	170-195
- length apophyses of lateral nematothecae	55-50	70-80	50-60	74-86
- length lateral nematothecae	75-85	80-95	75-95	74-88
- diameter of apical chamber of lateral nematotheca at rim	65-70	60-70	60-70	63-72

Geographical origin	Bali	Madagascar	Maldives	Guadeloupe, Martinique (*)
Reference(s)	Present study	Present study	Present study	Galea (2008); present study (*)
- length of mesial nematotheca	50-55	50-60	60-65	-
- diameter at rim of mesial nematotheca	45-50	45-55	50-55	-
- length of axillar nematotheca	40-55	35-40	35-40	-
- diameter of axillar nematotheca at rim	30-40	*ca.* 30	30-35	-
Gonotheca				
- length of pedicel	- (♂); - (♀)	45-60 (♂); 45-50 (♀)	- (♂); 50-60 (♀)	*ca.* 45 (♂); *ca.* 50 (♀) (*)
- length (excluding pedicel)	- (♂); - (♀)	430-625 (♂); 660-705 (♀)	- (♂); 585-670 (♀)	500-630 (♂); 695-730 (♀) (*)
- maximum width	- (♂); - (♀)	180-260 (♂); 390-425 (♀)	- (♂); 315-350 (♀)	195-275 (♂); *ca.* 330 (♀) (*)
- diameter at aperture	- (♂); - (♀)	55-70 (♂); 245-290 (♀)	- (♂); 205-240 (♀)	*ca.* 30 (♂) (*); *ca.* 225 (♀) (*)
- number of basal nematothecae	- (♂); - (♀)	2 (♂); 2 (♀)	- (♂); 2 (♀)	2 (♂); 2-3 (♀) (*)

Table 4. Various records approaching the phenotype of *Halopteris vervoorti* Galea, 2008, and their possible taxonomic status (L stands for length, Φ for diameter, Ho and He for homo- and heteromerous, respectively, and *Ha*., *He*. and *A*. for *Halopteris*, *Heterotheca* and *Antennella*, respectively).

	Billard (1913), *Siboga* Stn. 77, as *Ha. polymorpha*	**Vervoort (1966), as *Ha. polymorpha***	**Vervoort (1967), as *A. secundaria***	**Hirohito (1974), as *He. buski* (*sic!*)**	**Hirohito (1983), as *Ha. polymorpha***	**Ryland & Gibbons (1991), as *Ha. buskii* (BM1988.11.10.6-7)**	**Ryland & Gibbons (1991), as *Ha. buskii* (QM GL10293)**	**Hirohito (1995), as *Ha. buski* (*sic!*)**	**Preker & Lawn (2010), as *Ha. polymoprha***	**Preker & Lawn (2012), as *Ha. polymoprha***
Possible taxonomic status	Unsettled	Unsettled	(?) *Ha. vervoorti*	(?) *Ha. vervoorti*	Unsettled	(?) *Ha. vervoorti*	(?) *Ha. vervoorti*	(?) *Ha. vervoorti*	(?) *Ha. vervoorti*	Unsettled
Cormoids										
- geographical distribution	Indonesia	S Africa	Red Sea	Japan	Japan	Fiji	Fiji	Japan	Australia	Australia
- max. height (mm)	8	23	15	10	18	9	9	10	9	21
Caulus										
- segmentation	Ho	Ho	Ho	Ho	Ho	Ho	Ho	Ho	Ho	Ho
- axillar nematothecae	1	1	1	2	2	2	2	2	1	1
- nematothecae above hydroth.	?	1	Usually 1	1-2	1-2	< 3	< 3	1-2	2	2
Cladia										
- segmentation	He/Ho	Ho/He	He	He	Ho	He	He	He	He	He

	Billard (1913), *Siboga* Stn. 77, as *Ha. polymorpha*	Vervoort (1966), as *Ha. polymorpha*	Vervoort (1967), as *A. secundaria*	Hirohito (1974), as *He. buski* (*sic!*)	Hirohito (1983), as *Ha. polymorpha*	Ryland & Gibbons (1991), as *Ha. buskii* (BM1988.11.10.6-7)	Ryland & Gibbons (1991), as *Ha. buskii* (QM GL10293)	Hirohito (1995), as *Ha. buski* (*sic!*)	Preker & Lawn (2010), as *Ha. polymoprha*	Preker & Lawn (2012), as *Ha. polymoprha*
- nematoth. on 1st ahydroth. internode	1	1	1	1	1-2	1	1	1	-	-
- nematoth. on ordinary ahy-droth. inter-nodes	1 (occ. 2)	1 (on fused part)	1	1	1 (on fused part)	1	1	1	1 (rarely 2)	1-2
- axillar nematoth.	1	1	1	1 (exc. 2)	1-2	1 (occ. 2)	1 (occ. 2)	1	1	1
Measurements (µm)										
Caulus, L inter-node	-	-	270-325	-	-	360-380	265-325	-	320-420	498-1494
Cladia, L 1st ahydroth. intern.	245-270	-	-	-	-	-		-	-	66-100
Cladia, L ordi-nary ahydroth. intern.	190-255	Fused	130-140	-	Fused	130-140	100-150	-	150-260	282-415
Cladia, L hy-droth. intern.	310-365	675-1080 (fused)	245-250	-	- (fused)	190-240	175-230	-	260-340	249-315
Hydrotheca, L abaxial wall or Depth	215-230	240-255	190-215	*ca.* 270	260-270	175-210	150-180	180-220	112-180	183-249
Hydrotheca, L free adaxial wall	-	54-68	130-135	-	-	100-130	100-120	-	80-88	100-116
Hydrotheca, Φ aperture	175-190	245-270	150-165	*ca.* 160	260-270	160-180	160-185	180-200	152-160	149-189
Lateral nemato., L	-	55-60	-	-	-	-		-	-	50-100
Lateral nemato., Φ rim	-	45-55	-	-	-	-		-	-	42-83
Gonothecae, L	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	450-612 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	400-460 (♀)	- (♀)	- (♀)	- (♀)	558-738 (♀)	- (♀)	- (♀)	830-913 (♀)

	Billard (1913), *Siboga* Stn. 77, as *Ha. polymorpha*	**Vervoort (1966), as *Ha. polymorpha***	**Vervoort (1967), as *A. secundaria***	**Hirohito (1974), as *He. buski* (*sic!*)**	**Hirohito (1983), as *Ha. polymorpha***	**Ryland & Gibbons (1991), as *Ha. buskii* (BM1988.11.10.6-7)**	**Ryland & Gibbons (1991), as *Ha. buskii* (QM GL10293)**	**Hirohito (1995), as *Ha. buski* (*sic!*)**	**Preker & Lawn (2010), as *Ha. polymoprha***	**Preker & Lawn (2012), as *Ha. polymoprha***
Gonothecae, max. width	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	216-234 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	250-300 (♀)	- (♀)	- (♀)	- (♀)	252-360 (♀)	- (♀)	- (♀)	265-598 (♀)
Gonothecae, Φ aperture	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	45-54 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	- (♀)	- (♀)	- (♀)	- (♀)	162-234 (♀)	- (♀)	- (♀)	249-282 (♀)
Gonothecae, number of basal nematothecae	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	1 (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	2 (♀)	2 (♀)	- (♀)	- (♀)	2 (♀)	2-3 (♀)	- (♀)	2 (♀)

Table 5. Measurements (in μm) and main morphological features of *Halopteris australis* sp. nov., *H. millardae* sp. nov., and *H. brasiliensis* sp. nov.

	***Halopteris australis* sp. nov.**		***Halopteris millardae* sp. nov.**		***Halopteris brasiliensis* sp. nov.**
Geographical origin	New Caledonia	French Polynesia	Seychelles (*); Maldives	Zanzibar	Brazil
Reference(s)	Present study	Vervoort & Vasseur (1977), as *H. buskii*	Millard & Bouillon (1973) (*); Present study	Rees & Vervoort (1987), as *H. buskii* (Stn. 112)	Migotto (1996); present study (*)
Caulus (seen frontally)					
- maximum height (cm)	1.8	2.5	7 (*); 3.9	4.0	3.0
- segmentation	Ho (dist. He)	Ho	Ho	Ho	Ho
- superior nematothecae / internode with opposite cladia	2-3	-	3-4	-	2-3 (*)
- nematothecae above hydrotheca in ordinary internodes	1-2 (exc. 3), in two parallel rows	2, in two parallel rows	2-3 (exc. 4), in two parallel rows	2, in two rows	2 (occ. 1), in two parallel rows (*)
- number of axillar nematothecae	2 (rarely 1 distally)	1	1	1	2 (*)
- internode length	465-680	475-550	490-845	460-520	325-600
- diameter at node	45-105	100-125	110-220	270-320	110-180
- length of apophysis	100-115	-	85-110	-	75-85 (*)
- length of nematothecae	90-100	-	100-170	-	65-95 (*)
- diameter of nematothecae at rim	45-50	-	55-85	-	50-60 (*)

	Halopteris australis sp. nov.		*Halopteris millardae* sp. nov.		*Halopteris brasiliensis* sp. nov.
Cladia (seen laterally)				-	
- segmentation	He	He	He	He/Ho	He
- number of nematothecae on 1st ahydrothecate internode	1 (exc. 2)	1	2 (exc. 3), in two parallel rows	-	1
- nematothecae on ordinary ahydrothecate internodes	1	1	2 (exc. 4), in two parallel rows; distally 1	1	1
- number of axillar nematothecae	1 (rarely 2)	1	1	1	1 (rarely 2) (*)
- length of quadrangular segment	45-50	45-55	45-65	-	40-50 (*)
- length of 1st ahydrothecate internode	210-280	-	170-245	-	137-320
- length of ordinary ahydrothecate internodes	150-195	210-250	180-230	Fused 495-580	150-200
- length of hydrothecate internodes	290-390	320-335	340-370		240-440
- diameter at transverse node	35-40	-	60-65	115-120	50-70
- length of nematothecae	60-75	-	75-95	-	50-70 (*)
- diameter at rim of nematotheca	30-40	-	35-50	-	40-50 (*)
Hydrotheca (cladial)					
- shape of the rim (lateral view)	Distinctly sinuated	Distinctly sinuated	Slightly sinuated	Reportedly even	Even
- length abaxial wall	205-240	200-220	170-220	175-200	162-237
- length free adaxial wall	105-115	40-55	75-80	-	120-135 (*)
- diameter at rim	175-190	-	210-220	220-235	180-205
- length apophyses of lateral nematothecae	65-80	-	30-35	-	50-65 (*)
- length lateral nematothecae	90-100	85-95	85-110	95-140	75-125
- diameter of apical chamber of lateral nematotheca at rim	55-70	45-50	70-75	65-80	50-82
- length of mesial nematotheca	55-60	-	45-50	-	50-87
- diameter at rim of mesial nematotheca	45-50	-	35-40	-	35-60
- length of axillar nematotheca	45-50	-	20-30	-	40-50 (*)
- diameter of axillar nematotheca at rim	*ca.* 35	-	20-25	-	40-45 (*)
Gonotheca					
- length of pedicel	- (♂); *ca.* 70 (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); 75-80 (♀) (*)
- length (excluding pedicel)	- (♂); *ca.* 730 (♀)	- (♂); 400-420 (♀)	< 470 (♂) (*); < 1150 (♀) (*)	- (♂); - (♀)	- (♂); 800-910 (♀)
- maximum width	- (♂); *ca.* 340 (♀)	- (♂); 230-250 (♀)	< 210 (♂) (*); < 730 (♀) (*)	- (♂); - (♀)	- (♂); 310-450 (♀)
- diameter at aperture	- (♂); *ca.* 225 (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)
- number of basal nematothecae	- (♂); 2 (♀)	- (♂); 1 (♀)	1 (♂) (*) ; 2 (♀) (*)	- (♂); - (♀)	- (♂); 1-3 (♀)

1-2 superior nematothecae, arranged in one row, to be confined to their distal halves (Fig. 5C). Additional differences to other congeners are summarized in Appendix 1.

Distribution: Only known from Brazil (Migotto, 1996).

DNA SEQUENCE RESULTS AND DISCUSSION

The phylogenetic trees obtained with the Bayesian and the ML methods were largely identical and, therefore, only the ML is shown here (Fig. 9). The tree was rooted with the outgroup *Schizotricha frutescens* (comp. Peña Cantero *et al.*, 2010). The 16S gene is relatively rapidly evolving and, for Hydrozoa, it is only suitable for phylogenetic analyses at the specific and generic levels (comp. Leclère *et al.*, 2009). The genus *Antennella* appears clearly polyphyletic, as it has already been suggested by Schuchert (1997). Also, *Halopteris* appears to be polyphyletic and splits into at least two prominent clades. More detailed conclusions are not possible, mainly because samples of other important Halopterididae genera – *e.g. Corhiza* Millard, 1962 and *Gattya* Allman, 1885 – could not be obtained for the present analysis. Moreover, our study focuses on species delimitations.

Halopteris sibogae, raised to species level in the taxonomy section above, is clearly a distinct species and is not related to *H. polymorpha* (of which it was considered to be a mere variant). Likewise, *H. millardae* sp. nov. is also distinct from *H. polymorpha*, as was argued above. A Mediterranean sample (DG855922) formerly identified as *H. polymorpha* in Leclère *et al.* (2007) does not belong to this species, and is likely an as yet unnamed taxon. Despite coming from two different oceans, the samples of *H. vervoorti* clustered closely together. The two samples from the Atlantic and their two counterparts from the Indian Ocean map into two different subclades, but their divergences appear low, comparable to intraspecific divergences

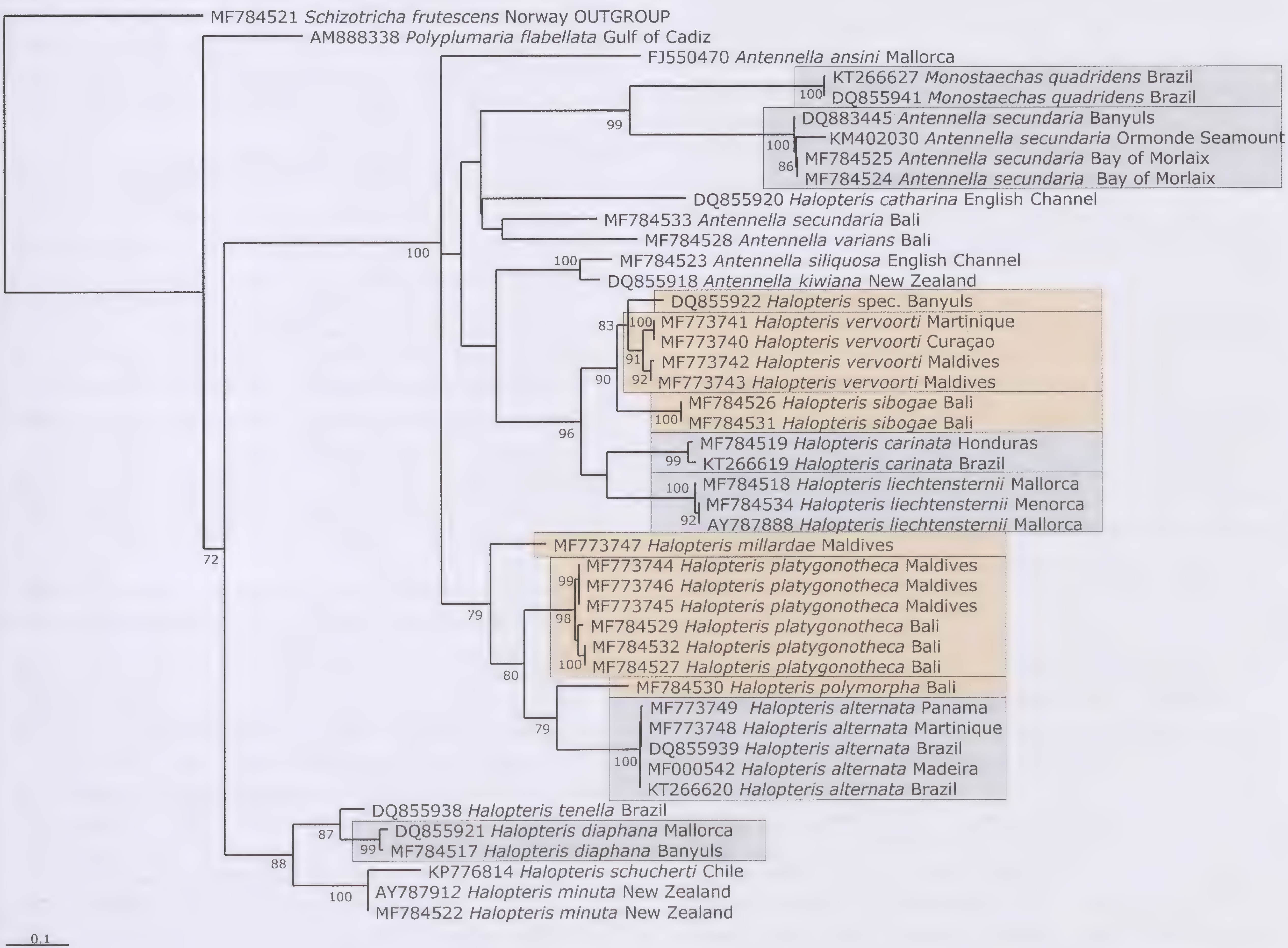

Fig 9. Maximum likelihood phylogenetic tree of Halopterididae species obtained with RAxML (GTR + G + I model) based on 547 bp positions (after Gblock treatment) of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details, see text and Appendix 2. Highlighted in yellow boxes are species discussed in the text, boxed in grey are other species clades with more than one sample, which permit to assess the intraspecific divergences observed in this family.

seen in other species clades (e. g. *H. platygonotheca* or *H. carinata* Allman, 1877). However, a more detailed analysis with more samples and markers is needed. *Halopteris platygonotheca* resembles morphologically *H. diaphana* (Heller, 1868), *H. tenella* (Verrill, 1874), and *H. alternata* (Nutting, 1900). Some of them have been considered conspecific, but they can be distinguished by the shape of the female gonotheacae (Schuchert, 1997). The 16S data confirmed that all four species are distinct and well separated. *Antennella secundaria* (Gmelin, 1791), as currently accepted, has a circumglobal distribution, but Schuchert (1997) suspected that it is a species complex. This was also observed with the 16S data, where the Indonesian sample of *A. secundaria* (MF784533) appears unrelated to its Atlantic counterparts.

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REFERENCES

Allman G.J. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, Assistant United States Coast Survey. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 5(2): 1-66.

Allman G.J. 1885. Description of Australian, Cape, and other Hydroida, mostly new, from the collection of Miss H. Gatty. *Journal of the Linnean Society of London, Zoology* 19: 132-161.

Allman G.J. 1888. Report on the Hydroida dredged by H.M.S. *Challenger* during the years 1873-76. Part II. – The Tubularinae, Corymorphinae, Campanularinae, Sertularinae and Thalamophora. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873-76, Zoology* 23(70): 1-90.

Ansín Agís J., Ramil F., Vervoort W. 2001. Atlantic Leptolida (Hydrozoa, Cnidaria) of the families Aglaopheniidae, Halopterididae, Kirchenpaueriidae and Plumulariidae collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands. *Zoologische Verhandelingen, Leiden* 333: 1-268.

Ansín Agís J., Vervoort W., Ramil F. 2009. Hydroids of the family Halopterididae (Cnidaria, Hydrozoa) collected in the western Pacific by various French expeditions. *Zoosystema* 31(1): 33-61.

Bale W.M. 1884. Catalogue of the Australian hydroid zoophytes. *Australian Museum, Sydney*, 198 pp.

Bedot M. 1921. Notes systématiques sur les Plumularides. 2e partie. *Revue suisse de Zoologie* 29(1): 1-40.

Billard A. 1911. Note préliminaire sur les espèces nouvelles de Plumulariidae de l'Expédition du Siboga. *Archives de Zoologie Expérimentale et Générale* (5)8: 62-71.

Billard A. 1913. Les hydroïdes de l'Expédition du Siboga. I. Plumulariidae. *Siboga-Expeditie* 7a: 1-115.

Billard A. 1918. Notes sur quelques espèces d'hydroïdes de l'Expédition du Siboga. *Archives de Zoologie Expérimentale et Générale* 57: 21-27.

Bouillon J., Gravili C., Pagès F., Gili J.M., Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1-591.

Bouillon J., Massin C., Kresevic R. 1995. Hydroidomedusae de l'Institut royal des Sciences naturelles de Belgique. *Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel*, 106 pp.

Busk G. 1852. An account of the Polyzoa and sertularian zoophytes collected in the voyage of the "Rattlesnake" on the coast of Australia and the Louisiade Archipelago, etc. (pp. 343-402). *In:* Macgillivray J. (ed). Narrative of the voyage of H.M.S. Rattlesnake commanded by the late Captain O. Stanley, R.N., F.R.S. etc., during the years 1846-1850. Vol. 1. *Boone T. & W., London*, 402 pp.

Calder D.R., Mallinson J.J., Collins K., Hickman C.P. 2003. Additions to the hydroids (Cnidaria) of the Galapagos, with a list of species reported from the islands. *Journal of Natural History* 37: 1173-1218.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540-552.

Coffroth M.A., Lasker H.R., Diamond M.E., Bruenn J.A., Bermingham E. 1992. DNA fingerprints of a gorgonian coral: a method for detecting clonal structure in a vegetative species. *Marine Biology* 114(2): 317-325.

Cornelius P.F.S. 1992. Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. *Scientia Marina* 56(2-3): 245-261.

Cunningham C.W., Buss L.W. 1993. Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae. *Biochemical Systematics and Ecology* 21: 57-69.

Darriba D., Taboada G.L., Doallo R., Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Di Camillo C.G., Bavestrello G., Valisano L., Puce S. 2008. Spatial and temporal distribution in a tropical hydroid assemblage. *Journal of the Marine Biological Association of the United Kingdom* 88(8): 1589-1599.

Galea H.R. 2006. On two new species of *Halopteris* Allman, 1877 (Cnidaria: Hydrozoa) from Chile. *Zootaxa* 1165: 57-68.

Galea H.R. 2007. Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile. *Zootaxa* 1597: 1-116.

Galea H.R. 2008. On a collection of shallow-water hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 1878: 1-54.

Galea H.R. 2010. Additional shallow-water thecate hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 2570: 1-40.

Galea H. R. 2013. New additions to the shallow-water hydroids (Cnidaria: Hydrozoa) from the French Lesser Antilles: Martinique. *Zootaxa* 3686(1): 1-50.

Galea H.R., Ferry R. 2015. Notes on some hydroids (Cnidaria) from Martinique, with descriptions of five new species. *Revue suisse de Zoologie* 122(2): 213-246.

Galea H.R., Schories D. 2012. Some hydrozoans (Cnidaria) from Central Chile and the Strait of Magellan. *Zootaxa* 3296: 19-67.

Galea H.R., Schories D., Försterra G., Häussermann V. 2014. New species and new records of hydroids (Cnidaria: Hydrozoa) from Chile. *Zootaxa* 3852(1): 1-50.

Gibbons M.J., Ryland J.S. 1989. Intertidal and shallow water hydroids from Fiji. I. Athecata to Sertulariidae. *Memoirs of the Queensland Museum* 27(2): 377-432.

Gmelin J.F. 1791. Vermes (pp. 3021-3910). *In:* Delamollière J.B. (ed). Caroli a Linné Systema naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis. Edition decima tertia, aucta reformata. Tom. I, Pars VI. *Lugduni*, XII+4120 pp.

Hartlaub C. 1901. Hydroiden aus dem Stillen Ocean. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896-97). *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie des Tiere* 14(6): 349-379.

Heller C. 1868. Die Zoophyten und Echinodermen des Adriatischen Meeres. *Verhandlungen der königlichen Zoologisch-Botanischen Gesellschaft von Wien* 18, supplement: 1-88.

Hirohito, Emperor of Japan. 1974. Some hydrozoans of the Bonin Islands. *Publications of the Biological Laboratory, Imperial Household, Tokyo*, 55 pp.

Hirohito, Emperor of Japan. 1983. Hydroids from Izu Ôshima and Niijima. *Publications of the Biological Laboratory, Imperial Household, Tokyo*, 83 pp.

Hirohito, Emperor of Japan. 1995. The hydroids of Sagami Bay. II. Thecata. *Publications of the Biological Laboratory, Imperial Household, Tokyo*, 244 pp (English text).

Johnston G. 1833. Illustrations in British Zoology (15. *Plumularia catharina*). *Magazine of Natural History* 6: 497-499.

Katoh K., Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772-780.

Kirchenpauer G.H. 1876. Ueber die Hydroidenfamilie Plumularidae, einzelne Gruppen derselben und ihre Fruchtbehälter. II. *Plumularia* und *Nemertesia*. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg* 6(2): 1-59.

Kirkendale L., Calder D.R. 2003. Hydroids (Cnidaria: Hydrozoa) from Guam and the Commonwealth of the Northern Marianas Islands (CNMI). *Micronesica* 35/36: 159-188.

Lamouroux J.V.F. 1816. Histoire des polypiers coralligènes flexibles vulgairement nommés zoophytes. *F. Poisson, Caen*, 560 pp.

Leclère L., Schuchert P., Manuel M. 2007. Phylogeny of the Plumularioidea (Hydrozoa, Leptothecata): evolution of colonial organization and life cycle. *Zoologica Scripta* 36: 371-394.

Leclère L., Schuchert P., Cruaud C., Couloux A., Manuel M. 2009. Molecular phylogenetics of Thecata (Hydrozoa, Cnidaria) reveals long-term maintenance of life history traits despite high frequency of recent character changes. *Systematic Biology* 58(5): 509-526.

Leloup E. 1940. Quelques hydropolypes de la baie de Sagami, Japon. (2e note). *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 16(19): 1-13.

Marktanner-Turneretscher G. 1890. Die Hydroiden des k. k. naturhistorischen Hofmuseums. *Annalen des k. k. Naturhistorischen Hofmuseums* 5: 195-286.

McCrady J. 1859. Gymnopthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221.

Migotto A.E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306: 1-125.

Millard N.A.H. 1962. The Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae. *Annals of the South African Museum* 46(11): 261-319.

Millard N.A.H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1-513.

Millard N.A.H. 1977. Hydroida. The South African Museum's Meiring Naude cruises. Part 3. *Annals of the South African Museum* 73(5): 105-131.

Millard N.A.H. 1978. The geographical distribution of southern African hydroids. *Annals of the South African Museum* 74(6): 159-200.

Millard N.A.H. 1980. The South African Museum's *Meiring Naude* cruises. Part 11. Hydroida. *Annals of the South African Museum* 82(4): 129-153.

Millard N.A.H., Bouillon J. 1973. Hydroids from the Seychelles (Coelenterata). *Annales du Muséum Royal de l'Afrique Centrale* 206: 1-105.

Millard N.A.H., Bouillon J. 1974. A collection of hydroids from Moçambique, East Africa. *Annals of the South African Museum* 65(1): 1-40.

Mulder J.F., Trebilcock R.E. 1909. Notes on Victorian Hydroida, with description of new species. *Geelong Naturalist* (2)4(1): 29-35.

Mulder J.F., Trebilcock R.E. 1911. Notes on Victorian Hydroida, with description of new species. (Continued). *Geelong Naturalist* (2)4(4): 115-124.

Nutting C.C. 1900. American hydroids. Part I. The Plumularidae. *Special Bulletin of the United States National Museum* 4(1): 1-285.

Nutting C.C. 1927. Report on the Hydroida collected by the United States Fisheries steamer "Albatross" in the Philippine region, 1907–1910. *In:* Contributions to the biology of the Philippine archipelago and adjacent regions. *Bulletin of the United States National Museum* 100(6)(3): 195-242.

Peña Cantero A.L., Sentandreu V., Latorre A. 2010. Phylogenetic relationships of the endemic Antarctic benthic hydroids (Cnidaria, Hydrozoa): what does the mitochondrial 16S rRNA tell us about it? *Polar Biology* 33(1): 41-57.

Pennycuik P.R. 1959. Marine and brackish water hydroids. *In:* Faunistic records from Queensland. Part V. *University of Queensland Papers, Department of Zoology* 1(6): 141-210.

Pictet C. 1893. Etude sur les Hydraires de la Baie d'Amboine. *Revue suisse de Zoologie* 1: 1-64.

Preker M. 2001. Hydroids from North East Cay, Herald Cays (pp. 151-156). *In:* Royal Geographical Society of Queensland Inc. (ed). Geography Monograph Series 6. Herald Cays Scientific Study Report. *Royal Geographical Society of Queensland Inc., Brisbane*, 168 pp.

Preker M. 2005. Notes on hydrozoans from North West Island. *Queensland Naturalist* 43(4-6): 46-50.

Preker M., Lawn I. 2005. Hydroids (Hydrozoa: Leptolida) from the Wellesley Islands, Gulf of Carpentaria (pp. 333-349). *In:* Geography Monograph Series 10. Gulf of Carpentaria Scientific Study Report. *Royal Geographical Society of Queensland Inc., Milton*, 390 pp.

Preker M., Lawn I.D. 2010. Hydroids (Cnidaria: Hydrozoa: Leptolida) from Moreton Bay, Queensland, and adjacent regions: a preliminary survey. *In:* Davie P.J.F. & Philips J.A. (eds). Proceedings of the Thirteen International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. *Memoirs of the Queensland Museum, Nature* 54(3): 109-149.

Preker M., Lawn I.D. 2012. Hydroids from the Heron Island reef flat. *Queensland Naturalist* 50(4-6): 32-58.

Ralph P.M. 1961. New Zealand thecate hydroids. Part IV. Family Plumulariidae. *Transactions of the Royal Society of New Zealand* 1(3): 19-74.

Redier L. 1966. Hydraires et bryozoaires. *In:* Fondation Singer-Polignac (ed). Contribution à l'étude des rivages coralliens d'après les récoltes de Yves Plessis, en Océanie (Mission Singer-Polignac). *Cahiers du Pacifique* 9: 78-122.

Rees W.J., Thursfield S. 1965. The hydroid collections of James Ritchie. *Proceedings of the Royal Society of Edinburgh* 69: 34-220.

Rees W.J., Vervoort W. 1987. Hydroids from the John Murray expedition to the Indian Ocean, with revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa). *Zoologische Verhandelingen, Leiden* 237: 1-209.

Ritchie J. 1909. Supplementary reports on the hydroids of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 47(1): 65-101.

Ritchie J. 1910. Hydroids from Christmas Island, Indian Ocean, collected by C. W. Andrews, D. Sc, F.R.S., F.Z.S., in 1908. *Proceedings of the Zoological Society of London* 1910: 826-836.

Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.

Ryland J.S., Gibbons M.J. 1991. Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaopheniidae. *Memoirs of the Queensland Museum* 30(3): 525-560.

Schuchert P. 1997. Review of the family Halopterididae. *Zoologische Verhandelingen, Leiden* 309: 1-162.

Schuchert P. 2015. *Halopteris* Allman, 1877. *In:* Schuchert P. (2017). World Hydrozoa database. Accessed at http://www.marinespecies.org/hydrozoa/aphia.php?p=taxdetails&id=117114 on 2017-06-05.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312-1313.

Stechow E. 1919. Zur Kenntnis des Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologische Jahrbücher* 42(1): 1-172.

Stechow E. 1923. Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. *Zoologischer Anzeiger* 56(1-2): 1-20.

Stechow E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer „Valdivia" 1898-1899* 27: 383-546.

Thornely L.R. 1904. Report on the Hydroida collected by Professor Herdman, at Ceylon, in 1902. *Ceylon Pearl Oyster Fisheries, Supplemental Report* 8: 107-126.

Thornely L.R. 1916. Report on the Hydroida collected by Mr. James Hornell at Okhamandal in Kattiawar in 1905-6 (pp. 147-150). *In:* Hornell J. (ed). Report to the Government of Baroda on the Marine Zoology of Okhamandal in Kattiawar, Part II. Williams and Norgate, London, XII + 165 pp.

Trebilcock R.E. 1928. Notes on New Zealand Hydroida. *Proceedings of the Royal Society of Victoria* 41(1): 1-31.

Van Soest R.W.M. 1976. A catalogue of the Coelenterate type specimens of the Zoological Museum of Amsterdam. II. Benthic Hydrozoa. *Beaufortia* 25(323): 79-95.

Vervoort W. 1941. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). *Temminckia* 6: 186-240.

Vervoort W. 1966. Bathyal and abyssal hydroids. *Scientific Results of the Danish Deep-Sea Expedition 1950-1952. Galathea Report* 8: 97-174.

Vervoort W. 1967. The Hydroida and Chondrophora of the Israel South Red Sea Expedition, 1962. *Israel South Red Sea Expedition, 1962* 25: 18-54.

Vervoort W., Vasseur P. 1977. Hydroids from French Polynesia with notes on distribution and ecology. *Zoologische Verhandelingen, Leiden* 159: 1-98.

Vervoort W., Watson J.E. 2003. The marine fauna of New Zealand: Leptothecata (Cnidaria: Hydrozoa) (thecate hydroids). *NIWA Biodiversity Memoir* 119: 1-538.

Verrill A.E. 1874. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical features of the region. *Report of the Commissioner of Fisheries for 1871-1872*: 295-747.

Von Schenck A. 1965. Die Kormentektonik der Plumulariiden (Coelenterata, Hydrozoa). *Revue suisse de Zoologie* 72(44): 855-1021.

Warren E. 1914. On the development of the planula in a certain species of plumularian hydroid. *Annals of the Natal Museum* 3(1): 83-102.

Watson J.E. 2000. Hydroids (Hydrozoa: Leptothecata) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museum and Art Galleries of the Northern Territory* 16: 1-82.

Watson J.E. 2005. Hydroids of the Archipelago of the Recherche and Esperance, Western Australia: annotated list, redescription of species and description of new species [pp. 495-611]. *In:* Wells F.E., Walker D.I. & Kendrick G. (eds). The Marine Flora and fauna of Esperance, Western Australia. *Western Australian Museum, Perth.*

Watson J.E. 2015. A new species of *Halopteris* (Hydrozoa: Leptothecata) and redescription of *Plumularia rotunda* from Victoria, Australia. *Memoirs of the Museum Victoria* 73: 41-46.

Zietara N.S., Arndt A., Geets A., Hellemans B., Volckaert F.A. 2000. The nuclear rDNA region of *Gyrodactylus arcuatus* and *G. branchicus* (Monogenea: Gyrodactylidae). *Journal of Parasitology* 86: 1368-1373.

Appendix 1. Comparative morphological features of several nominal *Halopteris* species.

Species name / color in life / geographical distribution / main references	**Caulus**		**Cladia**		**Hydrotheca**	**Lateral nematothecae**	**Female gonotheca**
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nemato-thecae	Shape	Length of apophyses / Relative length of theca / Shape of its upper chamber	Shape / Measurements / Number of basal nematothecae
***H. alternata* (Nutting, 1900)** / white / eastern and western Atlantic / Schuchert (1997); Galea (2008); present study	20 mm / Homomerous (occasionally heteromerous distally) / 1 median	1, displaced laterally	Heteromerous / Slightly longer than hydrothecate counterparts / 1	0	Conical, rim even, slightly flaring	Short / Not surpassing hydrothecal rim / Conical; adaxial wall uneven, either variably lowered or sinuated	Elongated-ovoid, lid perpendicular to longitudinal axis / up to 800 × 320 µm / 2
***H. australis* sp. nov.** / white / French Polynesia, New Caledonia / Vervoort & Vasseur (1977); Schuchert (1997); present study	25 mm / Homomerous (occasionally heteromerous distally) / 1-3 (5), displaced laterally	2, median	Heteromerous / Shorter than hydrothecate counterparts / 1	1-2	Conical, rim conspicuously sinuated	Long / Surpassing hydrothecal rim / Conical, adaxial wall sigmoid	Elongated-ovoid, tapering basally, lid perpendicular to longitudinal axis / *ca.* 730 × 340 µm / 2
***H. brasiliensis* sp. nov.** / yellowish / Migotto (1996); Schuchert (1997); present study	30 mm / Homomerous / 2 (occasionally 1) displaced laterally	2, median	Heteromerous / Shorter than hydrothecate counterparts / 1	1-2	Conical, rim even	Rather short / Not surpassing hydrothecal rim / Conical; adaxial wall sinuated	Broadly-ovoid, tapering basally, lid perpendicular to longitudinal axis / (800-910) × (310-450) µm / 1-3
***H. concava* (Billard, 1911)** / - / Indonesia, Philippines / Billard (1913); Ansín Agís *et al.* (2009); present study	60 mm / Homomerous / 6-7 displaced laterally	1, median	Homomerous / - / 2-3	1	Tubular, adaxial wall with distinct concavity; in frontal view distinctly swollen in middle	Relatively short / Barely surpassing hydrothecal rim / Globular; adaxial wall distinctly emarginated	Elongated-ovoid, lid oblique to longitudinal axis / (400-410) × (155-160) µm / 2
***H. crassa* (Billard, 1911)** / - / Indonesia, New Zealand / Billard (1913); Schuchert (1997)	150 mm / Homomerous / 2-4 displaced laterally	1, median	Homomerous / - / 0	1	Tubular on stem, conical on cladia; rim even	Relatively short / Reaching hydrothecal rim / Conical; adaxial wall emarginated	Elongated-ovoid, lid perpendicular to longitudinal axis / (1980-2150) × (840-910) µm / 2-5
***H. diaphana* (Heller, 1868)** / white / circumglobal in tropical and temperate seas / Schuchert (1997)	14 mm / Heteromerous / Generally 2 (occasionally 1 or 3) on ahydrothecate segments	0	Heteromerous / Longer than hydrothecate counterparts / 1	0	Conical, rim even	Very short / Not surpassing hydrothecal rim / Conical; adaxial wall occasionally emarginated	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / up to 700 µm long / 2-4
***H. glutinosa* (Lamouroux, 1816)** / brilliant scarlet / Australia, Tasman Sea, Indonesia, Japan / Schuchert (1997, as *H. buskii*); Watson (2005)	50 mm / Unsegmented (homomerous distally) / 1-4	1 (2 ?)	Homomerous (occasionally heteromerous) / 1 (rarely 2)	1	Conical, rim even	Well-developed / Reaching hydrothecal rim / Conical; deep adaxial emargination	Broadly ovoid, lid perpendicular to longitudinal axis, up to 12 nematothecae in 2 parallel rows / up to 1200 µm
***H. liechtensternii* (Marktanner-Turneretscher, 1890)** / pale straw to geenish / Mediterranean / Schuchert (1997); present study	27 mm / Homomerous (occasionally heteromerous distally) / 2-3 displaced laterally	2, median	Heteromerous / Shorter than, or as long as, hydrothecate counterparts / 1-2	1-2	Conical, rim even, slightly flaring	Well-developed / Reaching hydrothecal rim / Conical; rim either emarginated adaxially or sinuated	Elongated, nearly tubular, lid perpendicular to longitudinal axis / up to 1000 µm long / 2-3

Species name / color in life / geographical distribution / main references	**Caulus**		**Cladia**		**Hydrotheca**	**Lateral nematothecae**	**Female gonotheca**
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nemato-thecae	Shape	Length of apophyses / Relative length of theca / Shape of its upper chamber	Shape / Measurements / Number of basal nematothecae
***H. millardae* sp. nov.** / brownish / Seychelles, Maldives / Millard & Bouillon (1973); Schuchert (1997); present study	70 mm / Homomerous / 2-3 (4) displaced laterally	1, median	Heteromerous / Shorter than hydrothecate counterparts / 2 (occasionally 1 distally)	1	Conical, rim slightly sinuated	Rather short / scarcely reaching hydrothecal rim / Conical; sinuated adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / up to 1150 × 730 µm / 2
***H. minuta* (Trebilcock, 1928)** / - / New Zealand, French Polynesia / Schuchert (1997); Ralph (1961, as *H. constricta*)	9 mm / Heteromerous / 1 median, supra-axillar on hydrothecate internode + 1-2 median on ahydrothecate internode	0	Heteromerous / Shorter than hydrothecate counterparts / 1	0	Conical, rim even, slight adaxial concavity	Relatively short / Reaching hydrothecal rim / Conical; rim lowered on adaxial side	Strongly S-shaped, lid perpendicular to distal end of longitudinal axis, basal septum / (910-1000) × *ca.* 420 µm / 2
***H. nuttingi* (Billard, 1911)** / - / Indonesia, Australia, New Caledonia / Billard (1911, 1913); Schuchert (1997)	25 mm / Homomerous / 2-5 displaced laterally	1	Homo- and heteromerous / Of nearly the same length as their hydrothecate counterparts / 1-2	1	Conical, rim even	Relatively short / Not reaching hydrothecal rim / Globular, deeply scooped adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (740-810) × (310-365) µm / 2
***H. peculiaris* (Billard, 1913)** / - / Zanzibar, South Africa, Borneo / Billard (1913); Schuchert (1997)	90 mm / Homomerous / 2-3 displaced laterally	1	Homo- et heteromerous / When present, much shorter than hydrothecate counterpart / 0-1	1	Conical, rim even	Relatively short / Reaching hydrothecal rim / Conical, variably scooped adaxially, sometimes abaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (2000-2100) × (1040-1135) µm / 3
***H. platygonotheca* Schuchert, 1996** / pale-green / Comoros, Madagascar, Seychelles, Red Sea, Indonesia / Schuchert (1996); present study	40 mm / Homomerous (occasionally heteromerous distally) / 1-3 in a median row	0-1, median	Heteromerous / Slightly longer than hydrothecate counterparts / 1	0	Conical, rim even	Short / Not reaching hydrothecal rim / Conical; rim sinuated	Broadly ovoid, strongly flattened laterally, lid perpendicular to longitudinal axis / up to 1100 µm long / 2
***H. plumosa* Galea & Schories, 2012** / white / Chile, Argentina / Galea & Schories (2012); Galea *et al.* (2014)	34 mm / Homomerous (occasionally heteromerous distally) / 1-2 (rarely 3) displaced laterally	0	Homomerous in adult colonies, heteromerous in young ones / Much shorter than hydrothecate counterparts / 1 (exceptionally 2)	0	Tubular, curved adaxially, rim even	Rather short / Reaching hydrothecal rim / Conical; rim scooped adaxially	Strongly S-shaped, lid perpendicular to distal end of longitudinal axis, basal septum / *ca.* 860 × 455 µm / 2
***H. polymorpha* (Billard, 1913)** / yellow throughout/ Indonesia, Fiji / present study	37 mm / Homomerous / commonly 2-3 (range 1-5)	1, median	Heteromerous / Of nearly the same length / 1-2	0-1	Conical, shallow, rim even	Very short / Barely reaching hydrothecal rim / Conical; rim sinuated or emarginated adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (1015-1040) × (480-510) µm / 2-3
***H. pseudoconstricta* Millard, 1975** / - / South Africa, Angola, Vema Seamount, Three King Is. / Millard (1975); Schuchert (1997)	9 mm / Heteromerous / 1 median supra-axillar on hydrothecate internode + 1-2 median on ahydrothecate internodes	0	Heteromerous / Shorter than hydrothecate counterparts / 1-2 on ahydrothecate internode	0	Tubular, with distinct adaxial concavity, rim even; occasionally an internal adaxial projection of perisarc	Inconspicuous / Not reaching hydrothecal rim / Conical; rim even	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / up to 660 × 400 µm / 2
***H. regressa* (Billard, 1918)** / - / Indonesia / Billard (1918)	> 5 mm / Homomerous (heteromerous distally) / 1	0	Heteromerous / - / 1	0	Conical, rim supposedly even	Short / - / Globular; deeply scooped adaxially	Unknown

Species name / color in life / geographical distribution / main references	Caulus		Cladia		Hydrotheca	Lateral nematothecae	Female gonotheca
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nemato-thecae	Shape	Length of apophyses / Relative length of theca / Shape of its upper chamber	Shape / Measurements / Number of basal nematothecae
***H. schucherti* Galea, 2006** / white / Chile / Galea (2006)	75 mm / Homomerous / 1 median, supra-axillar + 6-8 displaced laterally	0	Homo- and heteromerous / When present, longer than hydrothecate counterparts/ 1 median proximal + 4-5 above	0	Conical, rim even	Very short / Not surpassing hydrothecal rim / Conical; variably scooped adaxially	Broadly ovoid, with S-shaped longitudinal axis, lid oblique, basal septum / (730-790) × (333-394) μm / 2
***H. sibogae* (Billard, 1913)** / yellow & white / Indonesia, Seychelles, Japan / present study	25 mm / Homomerous / 2-3 displaced laterally	1-2, median	Heteromerous / Shorter than hydrothecate counterparts / 1-2	1-2	Tubular, rim imperceptibly sigmoid in lateral view	Well-developed / Greatly surpassing hydrothecal rim / Conical; rim scooped adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (620-685) × (310-365) μm / 3
***H. simplex* (Warren, 1914)** / - / South Africa / Warren (1914); Millard (1975)	14 mm / Homomerous / 0	0	Heteromerous / Much shorter than hydrothecate counterparts / 1	0	Conical, rim even	Well-developed / Barely overtopping hydrothecal rim / Globular; emarginated on both ad- and abaxial sides	Piriform, flattened laterally, lid perpendicular to longitudinal axis / *ca.* 810 × 510 μm / 2
***H. tenella* (Verrill, 1874)** / white / southern California to Panama, Massachusetts to Caribbean, Brazil / Galea (2013); present study	50 mm / Heteromerous / 0-2 on hydrothecate internodes + 1-4 on ahydrothecate internodes, in almost a median row	0	Heteromerous / Much longer than hydrothecate counterparts / 1-2	0	Conical, rim even	Inconspicuous / Reaching hydrothecal rim / Conical; rim even	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / *ca.* 1335 × 370 μm / 3
***H. tuba* (Kirchenpauer, 1876)** / - / South Africa / Millard (1962); Schuchert (1997)	220 mm / Unsegmented for most of their length (homomerous distally) / 0	2, median	Homomerous / 0	1, naked	Forming two longitudinal rows along stem; conical, rim even	Well-developed / Greatly surpassing hydrothecal rim / Conical; rim even	Broadly ovoid, flattened laterally / (2950-3360) × (1510-1940) μm / 3
***H. urceolata* Watson, 2015** / white / Australia / Watson (2015)	15 mm / Heteromerous / 1 on ahydrothecate internodes	0	Heteromerous / - / 1 on ahydrothecate internode	0	Tubular, rim even, adaxial wall distinctly concave	Inconspicuous / Not reaching hydrothecal rim / Conical; rim even	Unknown
***H. vervoorti* Galea, 2008** / pale yellow to brownish / Lesser Antilles, Cape Verde, (?) Red Sea, Madagascar, Indonesia, Maldives, (?) Australia, (?) Japan, (?) Fiji / present study	20 mm / Homomerous (heteromerous distally) / 1-2 in a row	2 (distally 1), median	Heteromerous / Much shorter than hydrothecate counterparts / 1	1-2	Conical, rim even, slightly flaring, imperceptibly scooped laterally	Well-developed / Reaching hydrothecal rim / Conical; rim sinuated adaxially	Broadly ovoid, tapering below, lid perpendicular to longitudinal axis / (660-705) × (390-425) μm / 2
***H. violae* Calder *et al.*, 2003** / - / Galapagos / Calder *et al.* (2003)	23 mm / Homomerous (occasionally heteromerous distally) / 1 median + 2-4 displaced laterally	0	Heteromerous / Of same or slightly surpassing length / 1-2	0	Conical, rim even	Inconspicuous / Reaching hydrothecal rim / Conical; rim even	Elongated-ovoid, lid almost perpendicular to longitudinal axis / (600-700) × *ca.* 200 μm / 2

Appendix 2. Sample data used for the molecular analyses. GenBank numbers in bold are new sequences. nd = no data.

Species	GenBank accession number	Voucher	Locality	Latitude (+ N; - S)	Longitude (+ E; - W)	Collection date	Depth (m)
Antennella ansini	FJ550470	MHNG-INVE-32157	Mallorca, Spain	39.4518	3.2785	31.07.2001	3
Antennella kiwiana	DQ855918	MHNG-INVE-33623	Hauraki Gulf, New Zealand	-36.8123	174.8025	28.7.2002	0-1
Antennella secundaria	DQ883445	MHNG-INVE-32969	Banyuls-sur-Mer, France	42.5060	3.177	15.05.2002	62
Antennella secundaria	KM402030	DBUA1504.02	Ormonde seamount, Portugal	36.7143	-11.1661	10.06.2008	37-42
Antennella secundaria	**MF784524**	MHNG-INVE-79493	Baie de Morlaix, France	48.6763	-3.8842	30.08.2011	24-28
Antennella secundaria	**MF784525**	MHNG-INVE-89886	Baie de Morlaix, France	48.6768	-3.8861	10.09.2014	5-30
Antennella secundaria	**MF784533**	MHNG-INVE-97947	Bali, Indonesia	-8.3077	115.6208	02.02.2017	20
Antennella siliquosa	**MF784523**	MHNG-INVE-79490	Roscoff, France	48.7972	-3.9682	30.08.2011	70-75
Antennella varians	**MF784528**	MHNG-INVE-97931	Bali, Indonesia	-8.3560	115.6925	04.10.2016	0-20
Halopteris alternata	DQ855939	-	São Sebastião, Brazil	nd	nd	Sep. 2001	nd
Halopteris alternata	KT266620	MZUSP:1662	Barra de São Miguel, Brazil	-9.8333	-35.8847	22.10.2006	nd
Halopteris alternata	MF000542	MHNG-INVE-89422	Madeira, Portugal	32.8661	-17.1656	04.08.2014	0-2
Halopteris alternata	**MF773748**	HRG-1341	Martinique, France	14.6434	-61.1419	24.07.2017	1-2.5
Halopteris alternata	**MF773749**	DM&SM-BT014	Bocas del Toro, Panama	9.35	-82.23	30.07.2015	5
Halopteris carinata	KT266619	MZUSP:1681	Barra de São Miguel, Brazil	-9.7703	-35.8395	23.10.2006	nd
Halopteris carinata	**MF784519**	MHNG-INVE-35473	Honduras	16.0687	-86.9555	11.02.2004	20
Halopteris catharina	DQ855920	-	Roscoff, France	48.7300	-4.0000	April 1998	nd
Hal. aff. *polymorpha*	DQ855922	MHNG-INVE-30117	Banyuls-sur-Mer, France	42.5024	3.1273	23.06.1997	0-2
Halopteris diaphana	DQ855921	MHNG-INVE-30116	Mallorca, Spain	39.452	3.279	15.07.1997	nd
Halopteris diaphana	**MF784517**	MHNG-INVE-30118	Banyuls-sur-Mer, France	42.4803	3.1441	14.09.1995	2
Halopteris liechtesternii	AY787888	MHNG-INVE-29751	Mallorca, Spain	nd	nd	nd	nd
Halopteris liechtesternii	**MF784518**	-	Mallorca, Spain	-36.8123	174.8025	13.06.1997	1-3
Halopteris liechtesternii	**MF784534**	MHNG-INVE-97954	Menorca, Spain	40.0246	4.1936	26.05.2017	0-1
Halopteris millardae	**MF773747**	MHNG-INVE-98634	Faafu Atoll, Maldives	3.0649	72.9212	14.04.2016	35
Halopteris minuta	AY787912	MHNG-INVE-25073	Auckland, New Zealand	-36.8192	174.8068	14.10.1998	/
Halopteris minuta	**MF784522**	MHNG-INVE-88252	Auckland, New Zealand	-36.8192	174.8068	14.10.1998	/
Hal. platygonotheca	**MF773744**	DM&SM-MA0416141	Faafu Atoll, Maldives	3.0901	72.9679	18.04.2017	12
Hal. platygonotheca	**MF773745**	DM&SM-MA0416149	Faafu Atoll, Maldives	3.0938	72.9665	18.04.2017	13
Hal. platygonotheca	**MF773746**	DM&SM-MA0416168	Faafu Atoll, Maldives	3.0901	72.9679	20.04.2017	20
Hal. platygonotheca	**MF784527**	MHNG-INVE-97928	Bali, Indonesia	-8.2742	115.5926	29.09.2016	22

Species	GenBank accession number	Voucher	Locality	Latitude (+ N; - S)	Longitude (+ E; - W)	Collection date	Depth (m)
Hal. platygonotheca	**MF784529**	MHNG-INVE-97935	Bali, Indonesia	-8.3559	115.6925	04.10.2016	0-20
Hal. platygonotheca	**MF784532**	MHNG-INVE-97944	Bali, Indonesia	-8.2784	115.5970	31.01.2017	10-15
Halopteris polymorpha	**MF784530**	MHNG-INVE-97937	Bali, Indonesia	-8.5281	115.5148	06.10.2016	0-20
Halopteris schucherti	KP776814	MHNG-INVE-35930	Chile, Punta Huinay	-42.3745	-72.4281	09.03.2004	26.5
Halopteris sibogae	**MF784526**	MHNG-INVE-97926	Bali, Indonesia	-8.2742	115.5926	29.09.2016	22
Halopteris sibogae	**MF784531**	MHNG-INVE-97938	Bali, Indonesia	-8.5281	115.5148	06.10.2016	0-20
Halopteris tenella	DQ855938	-	São Sebastião, Brazil	-	-	-	-
Halopteris vervoorti	**MF773740**	DM&SM-CU005	Curaçao, The Netherlands	12.1214	-68.9692	09.06.2017	11
Halopteris vervoorti	**MF773741**	HRG-1339	Martinique, France	14.6434	-61.1419	24.07.2017	1-2.5
Halopteris vervoorti	**MF773743**	MHNG-INVE-98635	Faafu Atoll, Maldives	3.0761	72.9616	29.01.2016	3
Halopteris vervoorti	**MF773742**	MHNG-INVE-98636	Faafu Atoll, Maldives	3.0748	72.9663	13.04.2016	10
Monost. quadridens	DQ855941	-	Ilhabela, Brazil	-	-	Feb. 2002	nd
Monost. quadridens	KT266627	MZUSP:4632	Florianopolis, Brazil	-27.2280	-48.433	17.04.2008	nd
Polyplumaria flabellata	AM888338	-	Gulf of Cadiz, Morocco	35.17	-6.46	07.10.2006	451
Schizotricha frutescens	**MF784521**	MHNG-INVE-91725	Raunefjord, Norway	60.3382	5.1867	20.04.2015	30

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Novel molecular tools to identify *Plecotus* bats in sympatry and a review of their distribution in Switzerland

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Abstract: Three species of long-eared bats (*Plecotus auritus*, *P. macrobullaris* and *P. austriacus*) are known to occur in sympatry in Western Europe. They share very similar morphological characters that complicate their reliable discrimination. As a consequence, many records from these areas are reported to the generic level only and the exact distribution of species is uncertain. Even cranial characters are ambiguous since discriminant values traditionally used to identify those species vary with geography. We present a novel use of molecular tools to identify reliably the three cryptic species of long-eared bats. The methods proposed here for time- and cost-effective molecular identification of *Plecotus* species are applied to variously degraded samples such as ancient museum specimens and guano samples collected under roosts. We used this molecular approach to identify over 810 samples and reassess the distribution range of the three species occurring in Switzerland. We further showed that some skull measurements used for species recognition overlap to a greater extent than anticipated and can be misleading for morphologically intermediate individuals.

Keywords: Chiroptera - molecular identification - 16S - DNA barcoding - cryptic species - ancient DNA - forensic mammal identification.

INTRODUCTION

Three *Plecotus* species are present in Switzerland: the brown long-eared bat *Plecotus auritus* (Linnaeus, 1758), the alpine long-eared bat *P. macrobullaris* Kuzjakin, 1965 and the grey long-eared bat *P. austriacus* (J.B. Fischer, 1829). They are all threatened to the national level and listed in the Swiss Red List either as vulnerable, endangered or critically endangered, respectively (Bohnenstengel *et al.*, 2014). Since their densities, altitudinal preferences and habitat requirements vary greatly (Preatoni *et al.*, 2011; Razgour *et al.*, 2011; Ashrafi *et al.*, 2013), they certainly need specific measures of protection based on an exact knowledge of their distributions. Unfortunately, these species exhibit a conservative external morphology (Tvrtković *et al.*, 2005; Spitzenberger *et al.*, 2006; Ashrafi *et al.*, 2010), and highly similar or identical bioacoustic characteristics (Russo & Jones, 2002; Skiba, 2003; Middleton *et al.*, 2014; Barataud, 2015) that render unambiguous species recognition highly problematic. For these reasons, many field observations made in Europe in areas of sympatry are simply reported as "*Plecotus* sp." (Courtois *et al.*, 2011; LPO, 2014b; Gilliéron *et al.*, 2015), thus challenging the development of adequate conservation measures and management strategies to protect populations (Bickford *et al.*, 2007; Rutishauser *et al.*, 2012).

Multivariate analyses of many cranial characters have proven their ability to discriminate efficiently the different species of *Plecotus* (e.g. Spitzenberger *et al.*, 2006; Pavlinić & Đaković, 2015). However, such multivariate approaches require intact skulls to get all measurements and thus limit their use for more fragmentary material such as that recovered from mummies or from pellets of birds of prey. In an attempt to reduce the required measurements to a minimum number of characters, several authors (Bauer, 2001; Benda & Ivanova, 2003; Blant *et al.*, 2008) proposed identification keys concentrating on the best two discriminating variables, the largest diameter of the tympanic bullae (DBT) and maxillary tooth row length CM^3, but no molecular-based validation of the proposed criteria was performed. Such cranial or morphological identification methods in general were questioned. For instance, molecular reassessment of *Plecotus* distribution in Ticino could not confirm the presence of *P. austriacus* in the province (Mattei-Roesli, 2010) whilst the species was previously reported on the basis of morphological identifications (Maddalena & Moretti, 1994; Moretti *et*

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al., 2003) and suitable habitats apparently exist in the province (Rutishauser *et al.*, 2012).
Molecular tools are thus highly recommended to reliably assess species identification independently of morphology and ensure robustness of subsequent conclusions. The barcoding approach, whereby an unknown sample is sequenced for a standard DNA fragment (usually the mitochondrial cytochrome *c* oxidase subunit I, COI) and compared to a reference database (Hebert *et al.*, 2003), has been shown to be efficient for species recognition in European bats (Galimberti *et al.*, 2012). However, this approach requires time-consuming and relatively expensive methods to sequence the standard DNA fragment (657 bp). Furthermore, due to unknown stages of DNA degradation, it is often difficult or impossible to amplify such large fragments in ancient specimens or in guano samples of unknown age. Here, we present an efficient methodology particularly suited for the routine identification of old DNA samples of *Plecotus* bats. We apply this novel molecular approach to identify a large sample of museum specimens from Switzerland and neighbouring countries in order to evaluate the discriminatory power of the two cranial characters (DBT and CM^3) used in previous studies. We also implement this molecular approach to identify guano, tissue or mummy samples from Switzerland and provide a new picture of the distribution of the three species in this country.

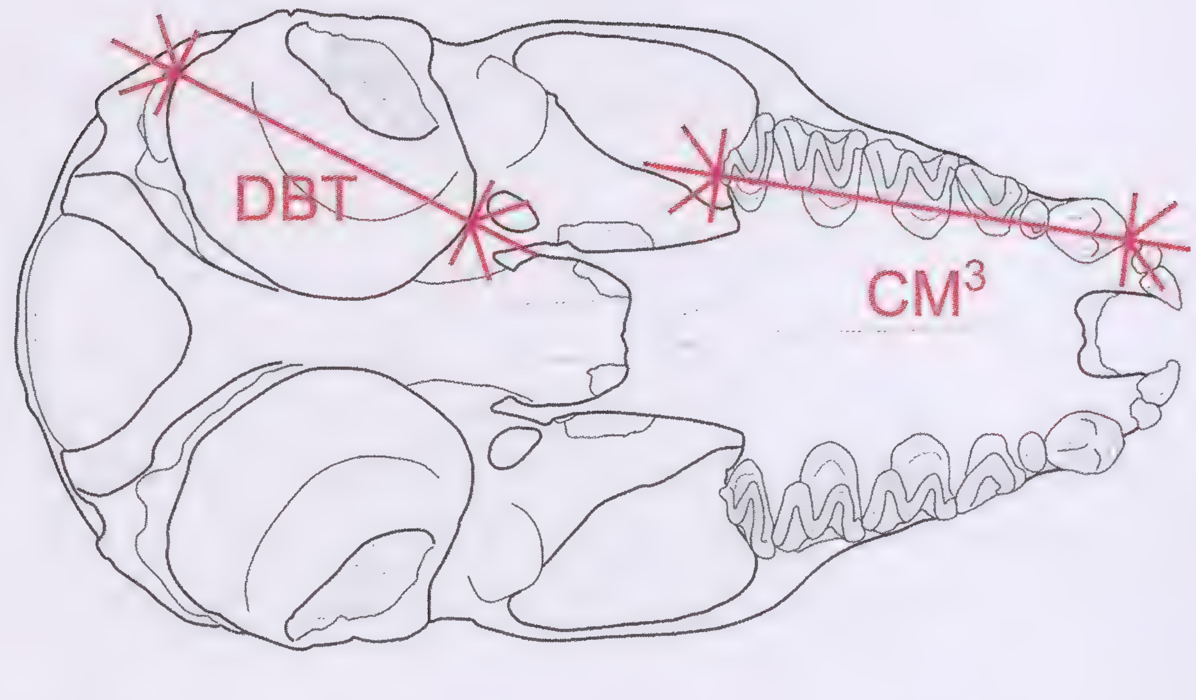

Fig. 1. Skull drawing of a *Plecotus austriacus* (specimen MHNG 1704.016) illustrating the two cranial measurements examined in this study (DBT and CM^3).

MATERIAL AND METHODS

Cranial measurements

The skulls of 194 adult specimens housed in the Natural History Museum of Geneva (MHNG) were examined, representing the three species *P. auritus* (n = 109), *P. austriacus* (n = 50) and *P. macrobullaris* (n = 40) (Appendix 1; DOI: 10.5281/zenodo.1041631). Specimens originated from Western Europe, primarily from Switzerland (n = 166) and France (n = 24). These skulls were measured with a digital calliper with accuracy of 0.01 mm for the following two measurements: DBT – maximum diameter of tympanic bulla, and CM^3 – mandibular tooth row length, measured from the canine to the third molar, without cingulum (Fig. 1). Statistical analyses were all carried out with standard functions implemented in R (R Core Team, 2017), and plot figures were produced using the ggplot2 package (Wickham, 2016).

Sampling and genomic DNA extraction

Our primary aim was to identify molecularly the three cryptic species of *Plecotus* living in sympatry in Switzerland issued from a variety of sources, such as faecal samples, old mummies, or ethanol-preserved museum materials. Guano samples were collected non-invasively under bat roosts, air-dried and then stored at room temperature in paper envelopes for periods ranging from several months to several years. Additional biopsy punches specifically sampled for monitoring programs were collected under appropriate licence and ethical approval (see Acknowledgments). Wing-membrane samples (3 mm in diameter) were collected with sterile biopsy punches according to standard procedures (Worthington-Wilmer & Barratt, 1996) and stored in ethanol. To further minimise the potentially stressful handling of live animals, minimal biological characteristics (gender, age, forearm and tibia length) and four standardised close-up pictures (profile, chin, thumb and foot) were taken. Animals were retained for a maximum of 20 min in cotton bags, before being released on the capture site.
As many samples contained only minute amounts of genetic material, DNA processing was done under a laminar flow hood sterilized with UV lights and with dedicated apparatus, to avoid cross-contamination. The tissue samples were extracted under sterile conditions using the DNeasy Blood & Tissue Kit (Qiagen, Switzerland) according to the manufacturer's protocol, whereas extracts from faecal samples were obtained with the DNA Stool Mini Kit (Qiagen, Switzerland) following the modifications suggested by Zeale *et al.* (2011). Purified DNA extracts were eluted in 200 μL of TE Buffer.
An initial group of 271 samples originating from Switzerland was sequenced for various fragments of the 16S gene (Appendix 2; DOI: 10.5281/zenodo.1041631). For the gel-based discrimination, we additionally attempted various amplifications with methods described below on 181 tissues and 97 guano extracts (Appendix 3; DOI: 10.5281/zenodo.1041631). We further assayed cross-amplifications on an array of ten other species of bats, including three other long-eared bats (*P. kolombatovici*, *P. teneriffae* and *P. gaisleri*) and several other genera of vespertilionids from the Western Palearctic region likely to share roosts with *Plecotus* (*Pipistrellus*, *Myotis*,

Eptesicus, *Vespertilio*, *Barbastella* and *Nyctalus*). As no tissue was available for *P. sardus*, we mined sequences from the GenBank (accession numbers AY175826, AY175822 and AY175819 from Mucedda *et al.*, 2002) in order to carry *in silico* alignments to estimate the cross-amplification specificity of our primers (see below).

Primer cocktails

In order to obtain size-specific amplicons that can be easily discriminated on agarose gels (see Kanuch *et al.*, 2007; Boston *et al.*, 2011), we first amplified reference samples of the three target species and sequenced them for a large fragment (540 bp) of the 16S gene in both directions, using the classical primers 16SAr and 16SBr (Palumbi *et al.*, 1991). These reference sequences were then aligned with the ClustalW algorithm (Thompson *et al.*, 1994) implemented in Sequencher 4.10.1 (Genecodes, USA). The same forward primer (16SAr) was used to amplify shorter, size-specific fragments, in combination with three newly designed reverse primers situated some 300-400 bp further downstream. The 16SauriR reverse primer matched exclusively sequences of *P. auritus*, the 16SaustR exclusively those of *P. austriacus* and the 16SmacrobR exclusively those of *P. macrobullaris*. Each of these new primers (Table 1) were designed to contain 5 to 8 specific mutations discriminating one species from the other two and were chosen to have a similar annealing temperature and no complementary 3' overlap with the other primers. These features allowed us to combine all three specific reverse and the forward primers in a single PCR cocktail in order to obtain size-specific amplicons.

Extracts containing only degraded DNA which either failed the PCR procedures described above or which were issued from guano samples of unknown age, were amplified for an even shorter fragment amplicon of the 16S gene (about 110 bp), using the primers MamP007F and MamP007R (Giguet-Covex *et al.*, 2014). This very short fragment was originally targeted to amplify ancient mammal DNA issued from soil samples, but its 79 hyper-variable nucleotide positions (Palumbi *et al.*, 1991) proved to have enough resolution for the discrimination of all species of *Plecotus*.

Amplifications

For the gel-based amplicon discrimination of the three target species, amplifications were achieved by multiplexing four primers (16SAr, 16SauriR, 16SaustR and 16SmacrobR) in a 25 µL reaction volume, including 2 µL 10× CoralLoad PCR Buffer (Qiagen, Switzerland), 1.6 µM $MgCl_2$, 0.16 mM dNTP, 0.1 µM of each primer, 4 µL Q-Solution, 0.5 U Taq Qiagen and 3 µL of extracted DNA. Owing to the different sources of DNA used, the DNA quantity and quality in the extract varied and different thermal cycling programs were necessary to optimize PCRs. For tissue extracts, containing typically 20-100 ng of bat DNA per µL, the cycling started with an initial denaturation at 94°C for 1.5 min, followed by 12 touchdown cycles consisting in 45 s denaturation at 94°C, 45 s annealing at a temperature set between 62 and 56°C (with a decreasing pitch of 0.5°C) and 1 min extension at 72°C, followed by 21 cycles with an annealing temperature set at 56°C and a final extension for 5 min at 72°C. For guano extracts, typically containing less than 2 ng of bat DNA per µL, the touchdown temperature was set between 58 to 52°C (with a decreasing pitch of 0.5°C) in order to provide less-stringent conditions for amplifications. These distinct annealing conditions were necessary to obtain only the targeted amplicons for older tissue samples and to be effective with guano extracts as well. To visualize the size-specific amplicons, 5 µL of PCR products were run for 30 minutes at 70 V on a 1.5% agarose gel containing 0.005% ethidium bromide. A 100 bp ladder (PeqLab, Germany) was run alongside the PCR products to estimate the size of the amplicons.

Amplification of the fragments intended to be sequenced was performed in a 25 µL reaction volume, including 2.5 µL CoralLoad PCR Buffer, 1.6 µM $MgCl_2$, 0.8 mM dNTP, 0.2 µM of each primer, 4 µL Q-Solution, 1 U

Table 1. Sequences and source of the different 16S primers used in this study. The amplicon size, expressed in number of base pairs (bp), corresponds to amplifications obtained with the 16Ar forward primer and one of the reverse primers. The MamP007 primer pairs produced an amplicon of about 110 bp.

Primer name	Sequence (5'-3')	Amplicon size	Reference
16SAr	CGCCTGTTTATCAAAAACAT		Palumbi *et al.* (1991)
16SBr	CCGGTCTGAACTCAGATCACGT	591 bp	Palumbi *et al.* (1991)
16auriR	GTTTAATTTGTCTCTTATAGATTAATGCTATAACTTG	291 bp	this study
16SaustR	GAGTTAGTCTTTATCTCGAGGTCG	352 bp	this study
16SmacrobR	TCATTGGCGGATCAATGTGTGG	416 bp	this study
MamP007F	CGAGAAGACCCTATGGAGCT		Giguet-Covex *et al.* (2014)
MamP007R	CCGAGGTCRCCCCAACC		Giguet-Covex *et al.* (2014)

Taq (Qiagen, Switzerland) and 3 µL of extracted DNA. Cycling conditions for MamP007F-MamP007R followed Giguet-Covex *et al.* (2014) and those for 16SAr-16SBr followed Mucedda *et al.* (2002). As they were short and easily read, the fragments were sequenced with the Sanger method in a single direction, using the forward primer used for amplification (either MamP007F or 16SAr).

Geographic range

Finally, all georeferenced specimens from Switzerland that could be identified molecularly (both here and in previous studies) were mapped on a 5 × 5 km grid in order to provide an updated view of the distribution of the three species living in this country. This map illustrates the six main biogeographical regions of Switzerland (i.e. Jura, Plateau, north side of the Alps, western inner Alps, eastern inner Alps and south side of the Alps, *sensu* Gonseth *et al.*, 2001).

RESULTS

Molecular identifications

A total of 278 DNA extracts of *Plecotus* spp. from various age and origins were tested for amplification with the species-specific primer cocktail. From these samples, 94/97 (97%) guano extracts, 74/74 (100%) wing biopsies and 61/107 (57%) ancient tissue extracts successfully amplified fragments of expected sizes. Of the failed samples, 45 were further tested for the very short amplicon with the MamP007 primers, which resulted in 35 (78%) positive PCR, all of which were successfully sequenced. The ten museum samples for which all our attempts to get amplification failed were most likely specimens that had been fixed in formalin before being stored in ethanol.

Overall, tissue samples tended to produce brighter bands than faecal material and were thus easier to discriminate on gels. The primer cocktail efficiently amplified a single product for *P. macrobullaris* and *P. austriacus* producing bright bands of about 400 and 350 bp, respectively (Fig. 2, lanes 1-2). For *P. auritus*, 126 of the 129 positive samples produced the expected single band at about 300 bp (Fig. 2, lane 3), but three samples produced a second band of about 400 bp (Fig. 2, lane 4). This unexpected double band pattern resulted from the primer 16SmacrobR (supposed to be specific to *P. macrobullaris*) annealing to sequences of *P. auritus* from Central and Eastern Europe. As shown by comparison with reference sequences, these *P. auritus* carry a different mitochondrial lineage from that of bats from Western Europe, that were called clades 'east' and 'west', respectively, by Juste *et al.* (2004). As these eastern *P. auritus* were the only bats resulting in a double-banded pattern on the agarose gels, this method thus allowed a simple discrimination of both lineages of *P. auritus*, and did not compromise other species identification.

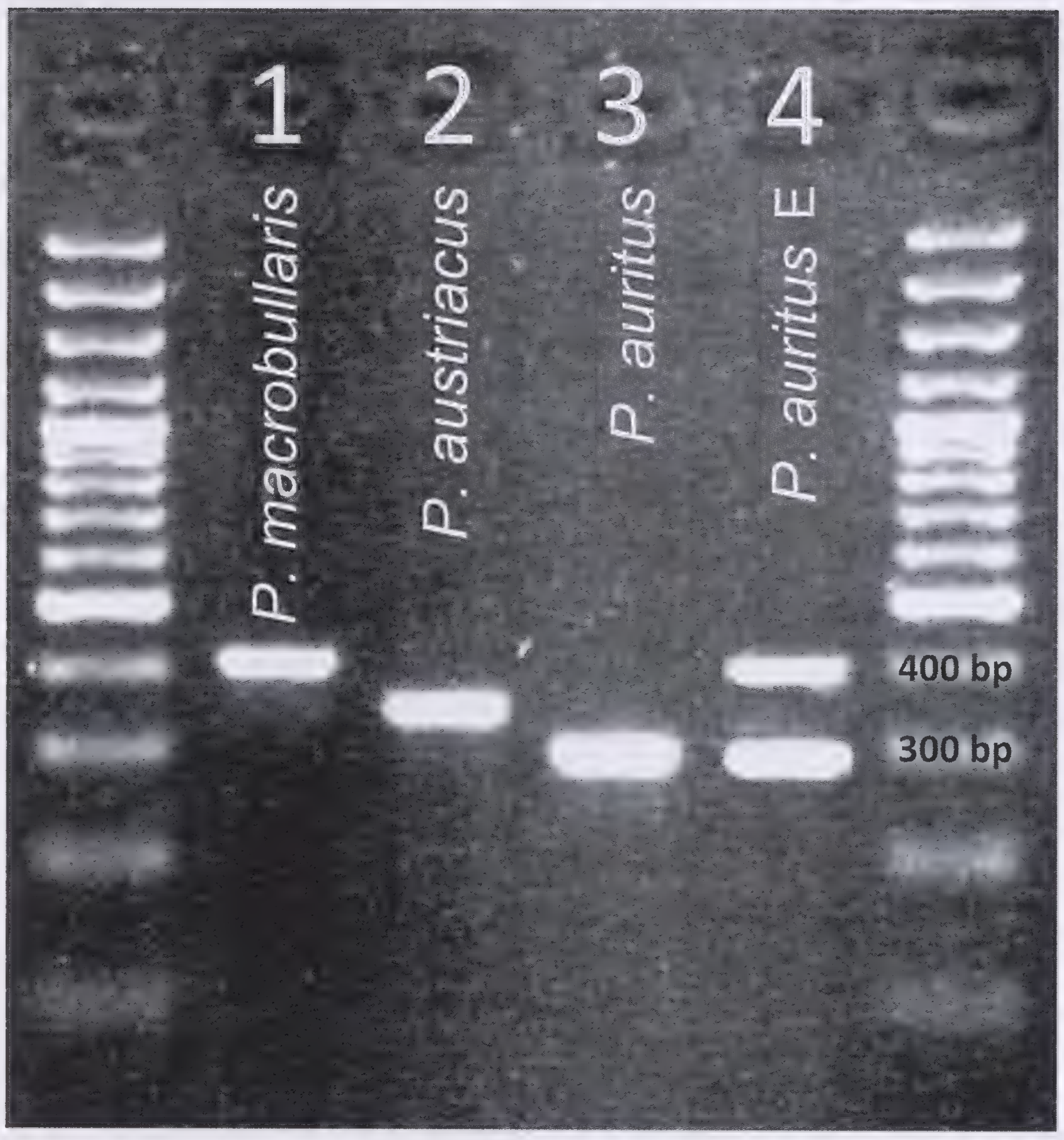

Fig. 2. Species-specific patterns of amplification of 16S fragments obtained in a single PCR cocktail. These fragments were resolved on a 1.6% agarose gel run for about 30 min at 60 V/m. A 100 bp molecular ladder was run on each side of the pictured agarose gel. Amplification products of diagnostic sizes appear on lane 1 for *P. macrobullaris* (at about 400 bp), on lane 2 for *P. austriacus* (350 bp), on lane 3 for the 'west' clade of *P. auritus* (300 bp) and on lane 4 for the 'east' clade of *P. auritus* (two bands at about 300 and 400 bp, respectively).

Cross-amplification of other bat species did not produce any visible band on the gel, even for extracts issued from good-quality tissue samples. The only exception was a very faint band of about 350 bp, i.e. in principle diagnostic for *P. austriacus*, obtained for one of the three *P. kolombatovici* tested (NMP 48725). Finally, in silico comparisons with *P. sardus* showed that none of the three specific reverse primers should amplify the 16S gene fragment for this species, as they all exhibit 3 to 5 mutations within the targeted annealing sequence.

Additional identifications and range reassessment

Additional samples from Switzerland (n = 271) were genetically identified using direct Sanger sequencing for full or partial 16S (see Appendix 2). Depending on the primers used, sequences ranged from 50 to 540 bp, and after alignment, were collapsed into seven unique haplotypes. The longest reads were deposited in the GenBank (accession numbers MF423092 to MF423098) and correspond to five distinct haplotypes of *P. auritus* (PaurHap1, 2, 3, 4 and 5), to a single haplotype of *P. austriacus* (PausHap1) and one of *P. macrobullaris*

(PmacHap1). Shorter reads were attributed to one of these seven haplotypes using a 100% matching score threshold (for a detailed list of specimens and haplotypes see Appendix 2). Besides these newly genotyped samples, 263 molecularly identified individuals (sequenced for either the COI or cyt-*b* mitochondrial genes) issued from previous publications (Ashrafi *et al.*, 2010; Mattei-Roesli, 2010; Rutishauser *et al.*, 2012) were also recovered to produce a total dataset of 700 *Plecotus* samples from Switzerland (Fig. 3). This comprehensive dataset includes 177 grid-cells occupied by *P. auritus*, 45 by *P. austriacus* and 82 by *P. macrobullaris*. These georeferenced and molecularly identified samples thus cover a large part of the country, except the northern slopes of the Alps, which are only marginally represented (Fig. 3). Thirteen grid-cells, mostly located in the Jura Mountain and Geneva province, have occurrences of both *P. auritus* and *P. austriacus*, and 17 from the inner and southern slopes of the Alps show sympatry between *P. macrobullaris* and *P. auritus*. A single grid-cell located in the Geneva province supports the molecular evidence for the sympatric occurrence of all three species in Switzerland.

Skull measurements

As expected, the measured skulls labelled as *P. auritus* in museum collections exhibited the smallest cranial dimensions, *P. austriacus* the greatest and *P. macrobullaris* intermediate values. Among the 194 studied skulls, 75 (39%) were associated with tissue samples that could be genetically identified (plain symbols in Fig. 4). The bivariate plot of the two cranial measurements overlaid with these molecular identifications shows that these dimensions overlap considerably among species, especially between *P. macrobullaris* and *P. austriacus* (Fig. 4). If one considers the limits proposed by Blant *et al.* (2008) to identify those skulls based on DBT and CM^3 (grey bars on Fig. 4), several molecularly identified specimens fall outside these limits and indeed were mislabelled in the museum collections. In particular, three molecularly identified *P. austriacus* with particularly small tooth rows (CM^3<5.7 mm in Appendix 1) would fall below the lowest values reported in this species (Spitzenberger *et al.*, 2002; Benda & Ivanova, 2003; Blant *et al.*, 2008). Conversely, due to its particularly large upper tooth row (CM^3=5.78 mm),

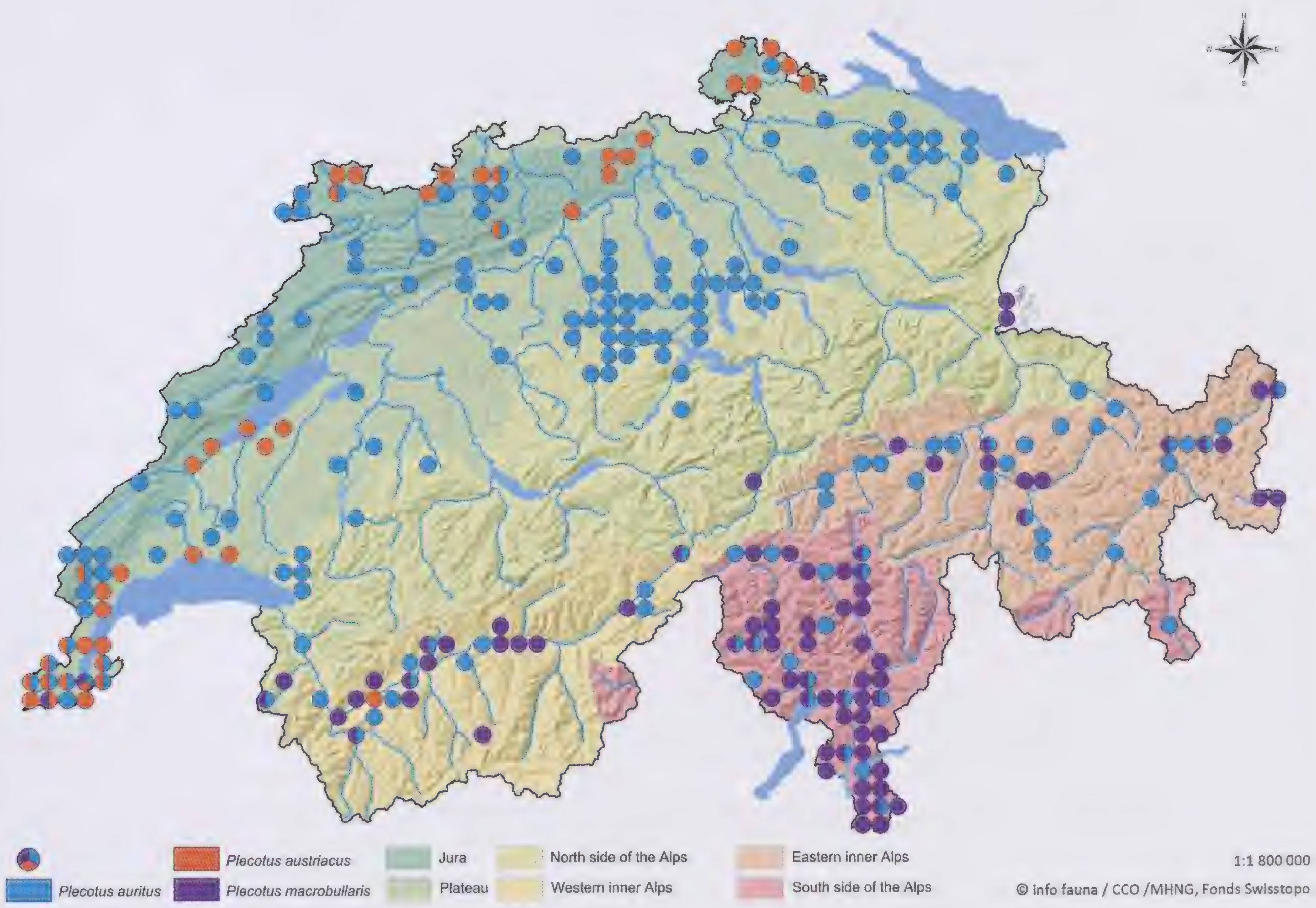

Fig. 3. Map of Switzerland depicting the six biogeographical regions occurring in this country (Gonseth *et al.*, 2001) and the occurrences of 700 genetically identified *Plecotus* samples. Plain symbols represent locations of *P. auritus* (in blue), *P. austriacus* (in orange) and *P. macrobullaris* (in violet). Symbols with more than one colour represent areas of sympatry. Map produced by the Centre Suisse de Cartographie de la Faune.

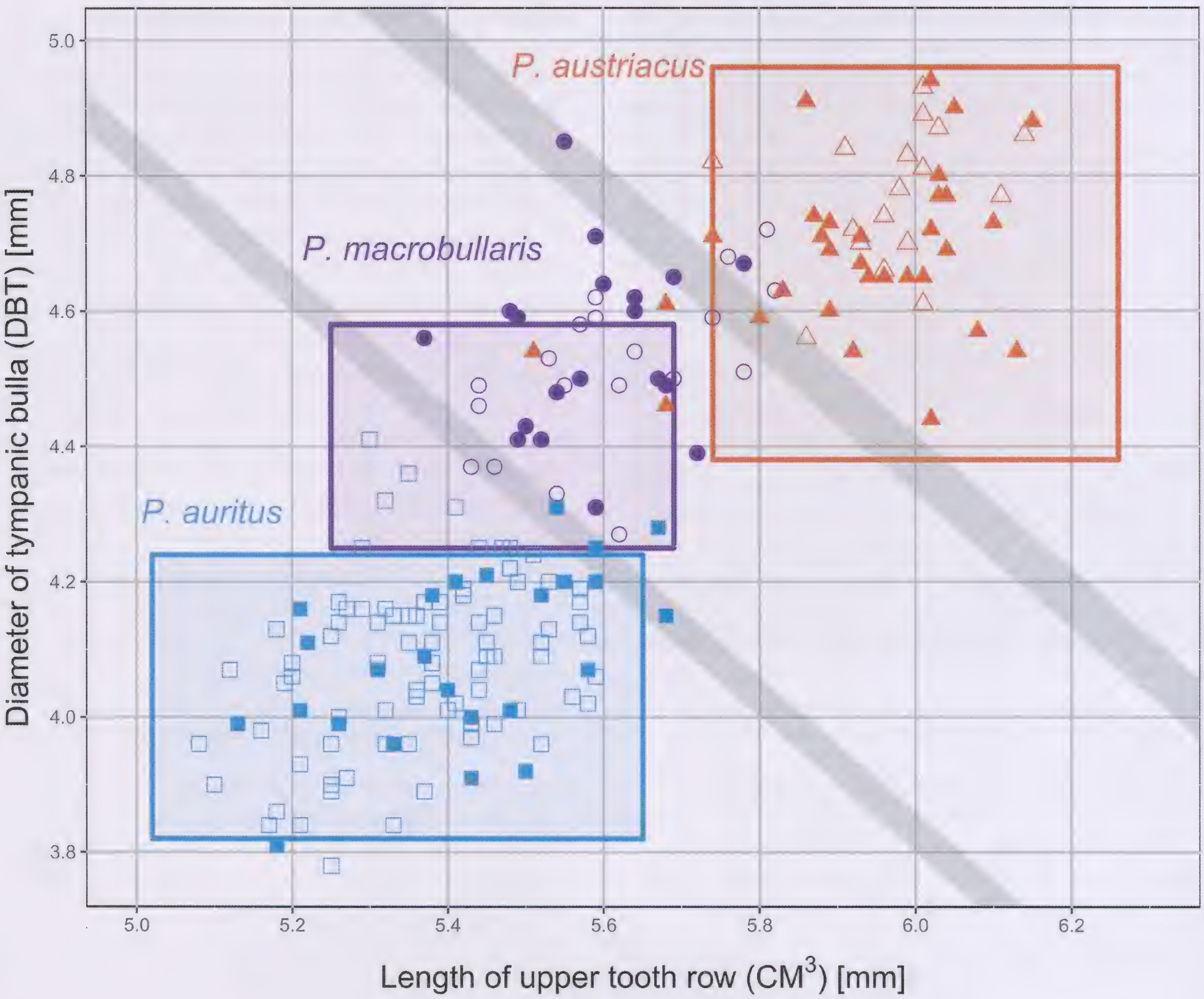

Fig. 4. Bivariate plot of the length of upper tooth row (CM^3) versus diameter of tympanic bulla (DBT) of 194 skulls of *Plecotus*. Blue squares represent skulls of *P. auritus*, violet circles skulls of *P. macrobullaris* and orange triangles skulls of *P. austriacus*. Plain symbols indicate genetically identified individuals, while hollow ones are from animals examined for skull morphology only. Coloured boxes indicate the species-specific measurement ranges given by Benda & Ivanova (2003) for Central European *Plecotus* and the grey bars represent the limit values of the two cranial measurements proposed by Blant *et al.* (2008) to identify the three species.

one genetically confirmed *P. macrobullaris* clearly falls within the morpho-space occupied by *P. austriacus*. A further *P. macrobullaris*, identified as such by external characters, had even greater dimensions (Fig. 4), but as it was fixed in formalin prior to storage in ethanol, its identification could not be confirmed genetically. We therefore suspect that more marginal records of genetically unverified animals on this scatter plot have doubtful identifications.

DISCUSSION

Molecular techniques

Reducing sequencing costs is desirable when financial resources are limiting, in particular for long-term monitoring programs of cryptic species, or when dealing with multiple non-invasive samples (such as faeces, hairs, etc.) that do not allow species recognition by other means than genetics. In the context of cryptic species recognition, cheaper methods based on gel discrimination of size-specific amplicons have been developed to circumvent these limitations (Kanuch *et al.*, 2007; Boston *et al.*, 2011). Similar protocols to save the purification and sequencing steps are proposed here, and provide a reliable, time- and cost-effective alternative that allows the discrimination of the three long-eared bat species in Switzerland. The new gel-based method also discriminates two major European lineages of *P. auritus* (the 'east' and 'west' lineages proposed by Juste *et al.*, 2004) by producing a unique double-banded pattern in the eastern lineage. Although we recommend to test the validity of this method with appropriate reference

samples when applied to other geographic areas (e.g. in the Iberian or Italian peninsulas, Ibáñez *et al.*, 2006; Galimberti *et al.*, 2012), it proved to be efficient in the Alpine region. It enabled routine identification of most samples and can be used to facilitate further studies where these long-eared bats occur in sympatry. The relatively small size of the amplicons makes this approach robust even for identifying mummies or relatively recent guano, which can be collected easily when monitoring roost occupancy without disturbing the colonies.

When the primer cocktail failed to amplify visible products on agarose gels, the amplification of an even shorter fragment (MamP007) was a good alternative to obtain usable PCR products. Although it implies the sequencing of the amplicons, this mini-16S fragment was successfully amplified in museum specimens stored in denatured ethanol for nearly half a century and in all guano samples of unknown age. This highly variable fragment was well-suited to discriminate all three species of *Plecotus* considered here, including the 'west' (corresponding to haplotypes PaurHap1 to 4 in Appendix 2) and 'east' (corresponding to PaurHap5) clades reported in *P. auritus* that only differ by few transitions in this fragment (Fig. 5). We thus strongly recommend the use of this mini-16S fragment when dealing with predictably low-quality DNA samples, e.g. those issued from necropsies. As this fragment amplifies a large array of other mammalian species as well (Giguet-Covex *et al.*, 2014), we anticipate that this versatile mini-16S fragment will be of much broader interest in forensic mammal identification. However, proper comprehensive reference sequences of all mammal species deposited in public repositories are currently lacking and hinder a quick identification based on this small 16S gene fragment. Thus, a more extensive use of this potentially well-discriminating marker is still awaiting the construction of more complete reference databases.

Critical evaluation of discriminant cranial characters

Several discriminant cranial measurements have been proposed to identify specimens of *Plecotus* in Western Europe (Häussler & Braun, 1991; Benda & Ivanova, 2003; Benda *et al.*, 2004; Spitzenberger *et al.*, 2006; Pavlinić & Đaković, 2015) including Switzerland (Blant *et al.*, 2008), but no independent identification method was used to validate their efficiency. By measuring DBT and CM^3 for a large number of skulls from Central Europe (n = 194), we show here that the three sympatric *Plecotus* do not cluster into distinct morpho-groups, but rather fall within a continuum of skull dimensions (Fig. 4). Furthermore, we could obtain genetic identification for 75 of the measured individuals with the genetic methods described here (plain symbols in Fig. 4), which suggest much more morphological overlap than anticipated. The skulls of *P. auritus* are indeed smaller and with a relatively small tympanic bulla, and barely overlap with the larger-sized *P. macrobullaris*. However, genetically identified *P. austriacus*, which have supposedly the largest dimensions in this morpho-space, fall clearly below the usual limits given for the species. Three small individuals of *P. austriacus* have the same dimensions as typical *P. macrobullaris* (Fig. 4) and thus would be misidentified if only those two skull measurements were used. These results stress the difficulty to identify the morphologically intermediate-sized *P. macrobullaris* based on skull characters only. Due to this large size overlap, there is probably no simple linear combination of skull measurements that would identify *P. macrobullaris* with certainty, and their discrimination is thus limited to the smallest and largest sections of this morpho-space (Fig. 4). Fortunately, if external characters can be examined, *P. macrobullaris* can be reliably recognised by the shape of the chin pad, as suggested by Spitzenberger *et al.* (2002) or Kiefer & Veith (2002). Indeed, all living individuals that were sampled here and identified a posteriori as *P. macrobullaris* by genetic methods had a typical triangular, laterally highly concave chin pad that

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                                   MamP007F
Consensus (from base 1 to 55)      CGAGAAGACCCTATGGAGCTTTAATTAAYTAACTTACAAGTTATAAYAATAATCT
Plecotus auritus 'west'            ............................T.............R..GC.T......
Plecotus auritus 'east'            ............................T.................C........
Plecotus macrobullaris             .....................C......C.......T.........T.C......
Plecotus austriacus                ............................C...T....G.A......T........
                                                                             MamP007R
Consensus (from base 56 to 110)    ATAAGAGACAAATYAAACTTGATTAAGTTAACAATTTRGGTTGGGGYGACCTCGG
Plecotus auritus 'west'            .............T......R................G.................
Plecotus auritus 'east'            .............T...............G.......A.................
Plecotus macrobullaris             .A...........C........C..............G.................
Plecotus austriacus                ......A.T...CC...A..A.....A...G......A................A
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Fig. 5. Alignment of typical 16S sequences of different *Plecotus* lineages obtained with the MamP007 primer pair (framed); the expected amplicon size is 110 bp (including primers). Alignment dots represent identical nucleotides.

was absent (or of a different shape) in the other species. To better illustrate this character, we compiled a range of close-ups from the three genetically identified species (Fig. 6).

The presence of few atypical specimens that conflict between a genetic and a morphologic diagnose (as shown in Fig. 4) raises a further question: are these animals just extremes in their cranial dimensions or do they represent interspecific hybrids? As all previous taxonomic studies (including this one) were based on mitochondrial markers (e.g. Mayer & Helversen, 2001; Kiefer *et al.*, 2002; Juste *et al.*, 2004; Spitzenberger *et al.*, 2006), which are inherited from the mother without contribution from the father (Ballard & Whitlock, 2004), they are not appropriate to detect the occurrence of putative interspecific hybrids (Andriollo *et al.*, 2015). Furthermore, cases of mitochondrial gene introgression are rare in bats, but at least known in few other vespertilionids (Berthier *et al.*, 2006; Artyushin *et al.*, 2009), and thus this phenomenon could also occur, albeit very rarely, in long-eared bats. The use of biparentally inherited markers such as nuclear microsatellites will be necessary to address this question in further studies.

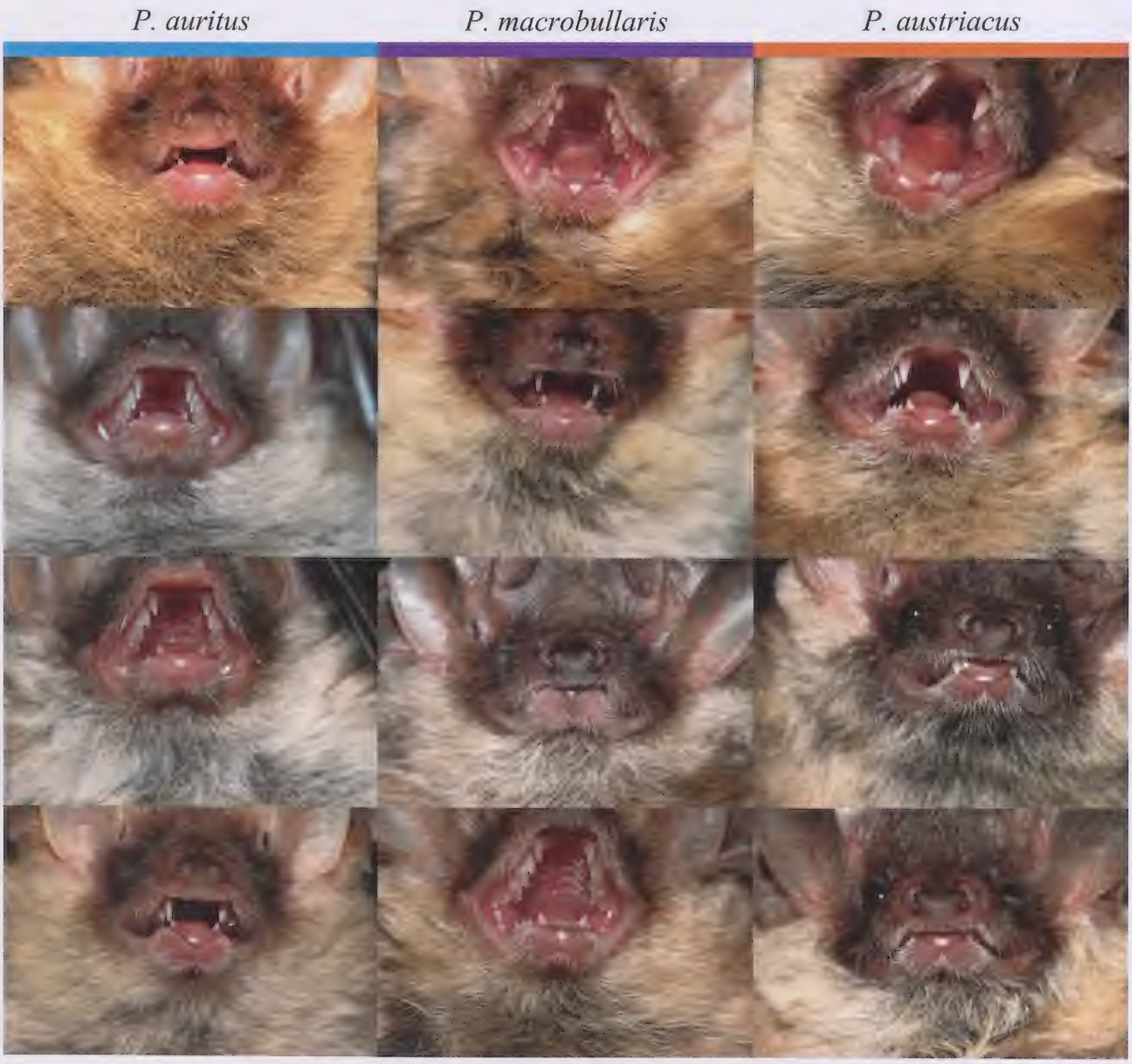

Fig. 6. Close-up views of the lower mandible of *Plecotus* bats illustrating the shape of the chin pad in the three species. Pictures were taken from genetically identified adult long-eared bats from Switzerland or France. In the first column is *P. auritus*, in the middle column *P. macrobullaris* and in the third *P. austriacus*. Notice the particular shape of the chin pad of *P. macrobullaris*, with elongated tip and distinctly concave sides.

Revised species ranges

Given that most previous distribution ranges of the three species of *Plecotus* in Switzerland were only based on morphology (Hausser, 1995) or in combination with genetic characters but on scattered localities (Mattei-Roesli, 2010; Rutishauser *et al.*, 2012), we compiled the occurrence of all genetically identified specimens (n = 429) with those already available from literature to provide a revised distribution map for the whole country (Fig. 3). Global geographic coverage is important as locally clumped occurrences might bias downstream model-based analyses such as ecological niche modelling (Rebelo *et al.*, 2012; Razgour *et al.*, 2013). One example is provided here by the geographically widespread *P. auritus*. Indeed, the modelled distribution for *P. auritus* issued from a more scattered sampling (Rutishauser *et al.*, 2012) essentially predicted that alpine valleys provided optimal habitats, with the Jura or the Swiss Plateau only marginally suitable for that species. Our revised distribution map, derived from genetically identified samples, shows instead that *P. auritus* is well represented in all biogeographic regions and the most common and widespread long-eared bat outside the Alpine range.

Despite its broad European distribution (Razgour *et al.*, 2013), *P. austriacus* is localised in Switzerland and considered a critically endangered species (Bohnenstengel *et al.*, 2014). Modelled distributions (Rutishauser *et al.*, 2012) predicted that the whole Plateau region should be suitable for that species, however we failed to confirm its presence over most of this region, despite an extensive sampling of guano pellets collected in more than 70 grid cells; all these samples proved to belong to *P. auritus* (Fig. 3). Given this sampling effort and the uncertainty of previous morphology-based identifications, *P. austriacus* seems to be truly absent from most of the central and oriental parts of the Swiss Plateau (Fig. 3). We also concur with Mattei-Roesli (2010) that this species is absent from the southern slopes of the Swiss Alps, where only *P. auritus* and *P. macrobullaris* can be found. Its absence from that region, as well as from the eastern inner Alps, is puzzling since appropriate habitats are available (Rutishauser *et al.*, 2012) and the species inhabits similar areas further away in neighbouring regions of Austria or France (Spitzenberger, 2001; LPO, 2014a). Although *P. austriacus* has been reported as nearly ubiquitous in Italy (Lanza, 2012), all records from the northern regions (e.g. Preatoni *et al.*, 2000) predate the recognition of *P. macrobullaris* (see Kiefer & Veith, 2002) and thus likely concern misidentifications, while a more recent survey in Piedmont did not recover this species (Debernardi & Patriarca, 2007). To the best of our knowledge, all genetically identified *P. austriacus* from Italy (Galimberti *et al.*, 2012; Razgour *et al.*, 2013) come from areas south of the Po river basin, i.e. well away from the Alps. Hence the northern limits of distribution of *P. austriacus* in Italy still need to be molecularly ascertained. For the Alpine region, Rutishauser *et al.* (2012) hypothesised this species might be outcompeted by *P. macrobullaris*, as an explanation for their parapatric distributions. The occurrence of stable colonies of all three species breeding sometimes within a radius of two kilometres in the Geneva province (Gilliéron *et al.*, 2015, Fig. 3) suggests that this hypothesis does not apply elsewhere. Furthermore, *P. austriacus* and *P. macrobullaris* also breed in sympatry in Corsica (Courtois *et al.*, 2011) without apparent competitive exclusion.

Our extended geographic sampling further confirms that most records of *P. macrobullaris* are from mountainous areas characterized by abrupt topology and fit the expectations of broad and fine-scale modelling conducted for the species across its entire range by Alberdi *et al.* (2014). In particular, it is well represented in inner valleys and southern slopes of the Alps (Mattei-Roesli, 2010; Ashrafi *et al.*, 2013) and is also confirmed from several valleys of the Graubünden province (Fig. 3). The altitudinal range occupied by molecularly identified *P. macrobullaris* might however be biased towards the most easily accessible roosts in the bottom of the valleys, as suggested by Alberdi *et al.* (2014). Hence, although extensive, the area covered by our sampling is still not ideal to be representative of the full regions occupied by the three species. Likewise, more samples from the northern slopes of the Swiss Alps should also be analysed for a complete understanding of the distribution of these species of *Plecotus* in Switzerland, and in particular to define the northern limits of occurrence of *P. macrobullaris*.

Despite these limitations, the increasingly efficient and relatively simple genetic methods proposed to identify cryptic species, including *Plecotus* bats as exemplified here, are providing more accurate distribution maps that will help develop better conservation strategies. These new methods also point to the need for better morphological diagnose for long eared-bats. One of the caveats mentioned earlier is the inability of such mitochondrially-based approaches to detect hybrid or introgressed individuals. This problem needs to be addressed with technologically more sophisticated approaches and is particularly needed for the areas where species ranges overlap (Fig. 3), and where hybridization might occur.

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REFERENCES

Alberdi A., Aizpurua O., Aihartza J., Garin I. 2014. Unveiling the factors shaping the distribution of widely distributed alpine vertebrates, using multi-scale ecological niche modelling of the bat *Plecotus macrobullaris*. *Frontiers in Zoology* 11: 014-0077. https://doi.org/10.1186/s12983-014-0077-6

Andriollo T., Naciri Y., Ruedi M. 2015. Two mitochondrial barcodes for one biological species: The case of European Kuhl's pipistrelles (Chiroptera). *Plos One* 10: e0134881. https://doi.org/10.1371/journal.pone.0134881.

Artyushin I.V., Bannikova A.A., Lebedev V.S., Kruskop S.V. 2009. Mitochondrial DNA relationships among North Palaearctic *Eptesicus* (Vespertilionidae, Chiroptera) and past hybridization between Common Serotine and Northern Bat. *Zootaxa* 2262: 40-52. https://doi.org/10.11646/zootaxa.2262.1.2

Ashrafi S., Bontadina F., Kiefer A., Pavlinić I., Arlettaz R. 2010. Multiple morphological characters needed for field identification of cryptic long-eared bat species around the Swiss Alps. *Journal of Zoology* 281: 241-248. https://doi.org/10.1111/j.1469-7998.2010.00697.x

Ashrafi S., Rutishauser M., Ecker K., Obrist M.K., Arlettaz R., Bontadina F. 2013. Habitat selection of three cryptic *Plecotus* bat species in the European Alps reveals contrasting implications for conservation. *Biodiversity and Conservation* 22: 2751-2766. https://doi.org/10.1007/s10531-013-0551-z

Ballard J.W.O., Whitlock M.C. 2004. The incomplete natural history of mitochondria. *Molecular Ecology* 13: 729-744. https://doi.org/10.1046/j.1365-294X.2003.02063.x

Barataud M. 2015. Acoustic ecology of European bats: species, identification, study of their habitats and foraging behaviour. *Biotope Editions, Mèze; Muséum national d'histoire naturelle, Paris*, 352 pp.

Bauer K. 2001. Bestimmungsschlüssel österreichischer Säugetiere anhand von Schädelmerkmalen [pp. 863-887]. *In:* Spitzenberger F. (ed). Die Säugetierfauna Österreichs, *Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Graz.*

Benda P., Ivanova T. 2003. Long-eared bats, genus *Plecotus* (Mammalia: Chiroptera), in Bulgaria: A revision of systematic and distributional status. *Casopis Narodniho muzea Rada prirodovedna* 172: 157-172.

Benda P., Kiefer A., Hanak V., Veith M. 2004. Systematic status of African populations of long-eared bats, genus *Plecotus* (Mammalia: Chiroptera). *Folia Zoologica* 53 (Monograph 1): 1-47. https://doi.org/10.3161/001.006.0202

Berthier P., Excoffier L., Ruedi M. 2006. Recurrent replacement of mtDNA and cryptic hybridization between two sibling bat species *Myotis myotis* and *Myotis blythii*. *Proceedings of the Royal Society B: Biological Sciences* 273: 3101-3109. https://doi.org/10.1098/rspb.2006.3680

Bickford D., Lohman D.J., Sodhi N.S., Ng P.K.L., Meier R., Winker K., Ingram K.K., Das I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution* 22: 148-155. https://doi.org/10.1016/j.tree.2006.11.004

Blant M., Magnin B., Ruedi M. 2008. Clé des crânes (Chiroptères) (pp. 132-145). *In:* Marchesi P., Blant M. & Capt S. (ed.). Mammifères de Suisse - Clés de détermination. *Fauna Helvetica, CSCF & SSBF, Neuchâtel, Switzerland*, Vol 21.

Bohnenstengel T., Krättli H., Obrist M.K., Bontadina F., Jaberg C., Ruedi M., Moeschler P. 2014. Liste rouge Chauves-souris. Espèces menacées en Suisse, état 2011. L'environnement pratique. *Office fédéral de l'environnement, Berne; Centre Suisse de Cartographie de la Faune, Neuchâtel; Centres suisses de coordination pour l'étude et la protection des chauves-souris, Genève et Zurich; Institut fédéral de recherches sur la forêt, la neige et le paysage, Birmensdorf*, 95 pp.

Boston E.S.M., Hanrahan N., Puechmaille S.J., Ruedi M., Buckley D.J., Lundy M.G., Scott D.D., Prodohl P. A., Montgomery W.I., Teeling E.C. 2011. A rapid PCR-based assay for identification of cryptic *Myotis* spp. (*M. mystacinus*, *M. brandtii* and *M. alcathoe*). *Conservation Genetics Resources* 3: 557-563. https://doi.org/10.1007/s12686-011-9404-9

Courtois J.-Y., Rist D., Beuneux G. 2011. Les chauves-souris de Corse. *Albiana*, 166 pp.

Debernardi P., Patriarca E. 2007. The bats of the Lake Maggiore Piedmont shore (NW Italy). *Hystrix* 18: 39-55.

Fischer, J. B. 1829. Synopsis Mammalium. *Cotta, Stuttgart*, 752 pp.

Galimberti A., Spada M., Russo D., Mucedda M., Agnelli P., Crottini A., Ferri E., Martinoli A., Casiraghi M. 2012. Integrated Operational Taxonomic Units (IOTUs) in echolocating bats: A bridge between molecular and traditional taxonomy. *Plos One* 7: e40122. ARTN e40122. https://doi.org/10.1371/journal.pone.0040122

Giguet-Covex C., Pansu J., Arnaud F., Rey P.-J., Griggo C., Gielly L., Domaizon I., Coissac E., David F., Choler P., Poulenard J., Taberlet P. 2014. Long livestock farming history and human landscape shaping revealed by lake sediment DNA. *Nature Communications* 5. https://doi.org/10.1038/ncomms4211

Gilliéron J., Schönbächler C., Rochet C., Ruedi M. 2015. Atlas des chauves-souris du bassin genevois. *CCO-Genève*, 262 pp.

Gonseth Y., Wohlgemuth T., Sansonnens B., Buttler A. 2001. *Les régions biogéographiques de la Suisse – Explications et division standard* (Office fédéral de l'environnement, des forêts et du paysage, Bern).

Hausser J. ed. 1995. Mammifères de la Suisse - Répartition, Biologie, Ecologie. *Birkhäuser Verlag, Basel, Switzerland*, 501 pp.

Häussler U., Braun M. 1991. Sammlung einheimischer Fledermäuse (Mammalia: Chiroptera) des Staatlichen Museums für Naturkunde Karlsruhe – Teil II: *Plecotus*. *Carolinea* 49: 101-114.

Hebert P.D.N., Cywinska A., Ball S.L., Dewaard J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270: 313-321. https://doi.org/10.1098/rspb.2002.2218

Ibáñez C., García-Mudarra J.L., Ruedi M., Stadelmann B., Juste J. 2006. The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica* 8: 277-297. https://doi.org/10.3161/1733-5329(2006)8[277:TICTCD]2.0.CO;2

Juste J., Ibàñez C., Muñoz J., Trujillo D., Benda P., Karatas A., Ruedi M. 2004. Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic Islands. *Molecular Phylogenetics and Evolution* 31: 1114-1126. https://doi.org/10.1016/j.ympev.2003.10.005

Kanuch P., Hajkova P., Rehak Z., Bryja J. 2007. A rapid PCR-based test for species identification of two cryptic bats *Pipistrellus pipistrellus* and *P. pygmaeus* and its application on museum and dropping samples. *Acta Chiropterologica* 9: 277-282. https://doi.org/10.3161/1733-5329(2007)9[277:ARPTFS]2.0.CO;2

Kiefer A., Veith M. 2002. A new species of long-eared bat from Europe (Chiroptera: Vespertilionidae). *Myotis* 39: 5-16. https://doi.org/10.3161/001.004.0202

Kiefer A., Mayer F., Kosuch J., Helversen O.V., Veith M. 2002. Conflicting molecular phylogenies of European long-eared bats (*Plecotus*) can be explained by cryptic diversity. *Molecular Phylogenetics and Evolution* 25: 557-566. https://doi.org/10.1016/S1055-7903(02)00299-3

Kuzjakin A. 1965. Otrjad Rukokrylyje. Ordo Chiroptera [pp. 79-116]. *In:* Bobrinskoj N., Kuznetsov B., Kuzjakin A. (ed.). *Opredelitel mljekopitayushtshikh SSSR, Isd. Prosveshtshenije, Moscow.*

Lanza B. 2012. Mammalia V : Chiroptera. *Calderini, Bologna*, 786 pp.

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Edition decima, reformata. Tomus I. Laurentii Salvii, Holmiae, ii + 824 pp.

LPO 2014a. Oreillard gris. *Plecotus austriacus* (J.B. Fischer, 1829) (pp. 362-369). *In:* LPO (ed.). Les chauves-souris de Rhône-Alpes, *LPO Rhône-Alpes, Lyon*.

LPO 2014b. Oreillards indéterminés. *Plecotus spp.* (pp. 352-353). *In:* LPO (ed). Les chauves-souris de Rhône-Alpes, *LPO Rhône-Alpes, Lyon*.

Maddalena T., Moretti M. 1994. Identificazione biochimica e morfologica di due specie sorelle: *Plecotus auritus* e *Plecotus austriacus* (Chiroptera: Vespertilionidae). (Centro Svizzero di coordinamento per lo studio e la protezione dei pipistrelli; Ufficio Protezione Natura del Canton Ticino – Dipartimento del territorio).

Mattei-Roesli M. 2010. Situazione del genere *Plecotus* (Chiroptera) nel Cantone Ticino (Svizzera). *Bollettino della Società ticinese di Scienze naturali* 98: 31-34.

Mayer F., Helversen V.O. 2001. Cryptic diversity in European bats. *Proceedings of the Royal Society B: Biological Sciences* 268: 1825-1832. https://doi.org/10.1098/rspb.2001.1744

Middleton N., Froud A., French K. 2014. Social calls of the Bats of Britain and Ireland. *Pelagic Publishing Ltd.*

Moretti M., Roesli M., Gamboni A.-S., Maddalena T. 2003. I pipistrelli del Cantone Ticino. *Memorie della Società ticinese di scienze naturali* 6: 1-91.

Mucedda M., Kiefer A., Pidinchedda E., Veith M. 2002. A new species of long-eared bat (Chiroptera: Vespertilionidae) from Sardinia (Italy). *Acta Chiropterologica* 4: 121-135. https://doi.org/10.3161/001.004.0202

Palumbi S.R., Kewalo A.M., Romano S., Mcmillan W.O., Stice L., Grabowski G. 1991. The Simple Fool's Guide to PCR. *University of Hawaii, Honolulu.*

Pavlinić I., Đaković M. 2015. Identification of four *Plecotus* species (Chiroptera, Vespertilionidae) in Croatia based on cranial characters. *Mammalia* 80: 385-394. https://doi.org/10.1515/mammalia-2014-0031

Preatoni D.G., Martinoli A., Zilio A., Penati F. 2000. Distribution and status of Bats (Mammalia, Chiroptera) in alpine and prealpine areas of Lombardy (Northern Italy). *Il Naturalista Valtellinese* 11.

Preatoni D.G., Spada M., Wauters L.A., Tosi G., Martinoli A. 2011. Habitat use in the female Alpine long-eared bat (*Plecotus macrobullaris*): does breeding make the difference? *Acta Chiropterologica* 13: 355-364. https://doi.org/10.3161/150811011x624820

R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Razgour O., Clare E.L., Zeale M.R.K., Hanmer J., Schnell I.B., Rasmussen M., Gilbert T.P., Jones G. 2011. High-throughput sequencing offers insight into mechanisms of resource partitioning in cryptic bat species. *Ecology and Evolution* 1: 556-570. https://doi.org/10.1002/ece3.49

Razgour O., Juste J., Ibáñez C., Kiefer A., Rebelo H., Puechmaille S.J., Arlettaz R., Burke T., Dawson D. A., Beaumont M., Jones G. 2013. The shaping of genetic variation in edge-of-range populations under past and future climate change. *Ecology Letters* 16: 1258-1266. https://doi.org/10.1111/ele.12158

Rebelo H., Froufe E., Brito J.C., Russo D., Cistrone L., Ferrand N., Jones G. 2012. Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modelling. *Molecular Ecology* 21: 2761-2774. https://doi.org/10.1111/j.1365-294X.2012.05566.x

Russo D., Jones G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology* 258: 91-103. https://doi.org/10.1017/s0952836902001231

Rutishauser M. D., Bontadina F., Braunisch V., Ashrafi S., Arlettaz R. 2012. The challenge posed by newly discovered cryptic species: disentangling the environmental niches of long-eared bats. *Diversity and Distributions* 18: 1107-1119. https://doi.org/10.1111/j.1472-4642.2012.00904.x

Skiba R. 2003. Europäische Fledermäuse. Kennzeichen, Echoortung und Detektoranwendung. Bd. 648. *Westrap Wissenschaften, Hohenwarsleben, Germany*, 212 pp.

Spitzenberger F. 2001. Die Säugetierfauna Österreichs. 13. *Bundesministerium für land-und Forstwirtschaft Umwelt and Wasserwirtschaft, Gratz, Austria*, 895 pp.

Spitzenberger F., Haring E., Tvrtković N. 2002. *Plecotus*

microdontus (Mammalia, Vespertilionidae), a new bat species from Austria. *Natura Croatica* 11: 1-18.

Spitzenberger F., Strelkov P., Winkler H., Haring E. 2006. A preliminary revision of the genus *Plecotus* (Chiroptera, Vespertilionidae) based on genetic and morphological results. *Zoologica Scripta* 35: 187-230. https://doi.org/10.1111/j.1463-6409.2006.00224.x

Thompson J.D., Higgins D.G., Gibson, T.J. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673-4680. https://doi.org/10.1093/nar/22.22.4673

Tvrtković N., Pavlinić I., Haring E. 2005. Four species of long-eared bats (*Plecotus*, Geoffroy, 1818; Mammalia, Vespertilionidae) in Croatia: field identification and distribution. *Folia Zoologica* 54: 75-88.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. *Springer International Publishing,* 260 pp.

Worthington-Wilmer J., Barratt E. 1996. A non-lethal method of tissue sampling for genetic studies of Chiropterans. *Bat Research News* 37: 1-3.

Zeale M.R., Butlin R.K., Barker G.L., Lees D.C., Jones G. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology Resources* 11: 236-244. https://doi.org/10.1111/j.1755-0998.2010.02920.x

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Second discovery of the subdichthadiigyne in *Yunodorylus* (Borowiec, 2009) (Formicidae: Dorylinae)

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Abstract: The genus *Yunodorylus* comprises four named species known exclusively from the Indo-Chinese and Indo-Malayan subregions. The queen and male of the genus were unknown until recently. However, the subdichtadiigyne was firstly discovered from two colonies of *Y. eguchii* (Borowiec, 2009), and described by Eguchi *et al.* in 2016. Then, the present authors discovered a colony of *Yunodorylus doryloides* (Borowiec, 2009) with a subdichthadiigyne and herein describe the subdichthadiigyne. The subdichtadiigyne of *Y. doryloides* is morphologically similar to that of *Y. eguchii*, but it can be distinguished by the combination of the following morphological characters: mandible elongate and slender, with the edge behind the basalmost tooth of the masticatory margin almost straight; lateroclypeal teeth rounded; mesosoma in dorsal view slenderer in the former than in the latter; mesonotum in dorsal view distinctly longer than broad in the former, but almost as long as broad in the latter; anterior margin of mesopleuron without a small lobe; metanotal groove in dorsal view faintly recognized; ventral margin of metapleuron almost straight; petiole in dorsal view narrower and longer in the former than in the latter; pygidium apically without any specialized setae.

Keywords: Dorylinae - *Yunodorylus doryloides* - queen - Borneo - Indo-Malayan region.

INTRODUCTION

The ant genus *Yunodorylus* Xu, 2000 is the only non-army doryline ant with a single waist segment and no or very weak girdling constriction on abdominal segment IV (Borowiec, 2016). This genus was once synonymized with the genus *Cerapachys* F. Smith, 1857 by Bolton (2003), but very recently it was assigned to the subfamily Dorylinae, and revived as an independent genus (Brady *et al.*, 2014; Borowiec, 2016). The genus contains four named species and has so far been known exclusively from the Indo-Chinese and Indo-Malayan subregions (Borowiec, 2009). The queen and male of the genus were unknown until recently: Borowiec (2016) provided a diagnosis and full description of the male based on an undetermined species, and Eguchi *et al.* (2016) described the queen of *Y. eguchii* (Borowiec, 2009) which is interestingly subdichthadiiform. The morphological features as well as behavioral features of two queen-right colonies of *Y. eguchii* (Mizuno *et al.,* in prep.) suggest an independent evolution of the “Army Ant Adaptive Syndrome” in the *Yunodorylus* lineage.

At the almost same time as the publication of Eguchi *et al.* (2016), the first author of the present paper (R. Satria) collected a queen-right colony of *Yunodorylus doryloides* (Borowiec, 2009) in Lambir Hills National Park, Miri, Sarawak, Malaysia (colony no. RS-55-LMB16). The queen was also subdichthadiiform similar to that of *Y. eguchii.* Unfortunately, with regulations relating to the use of biological specimens obtained in Sarawak, Malaysia, the colony could not be kept alive. Therefore, herein we describe external morphology of the subdichthadiigyne and provide information on the habitat in which *Y. doryloides* was found.

MATERIALS AND METHODS

Abbreviations of specimen depositories are as follows: MHNG, Muséum d’histoire naturelle, Geneva, Switzer-

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land; SFDC, Sarawak Forest Department Collection, Kuching, Sarawak, Malaysia. Species determination of the colony RS-55-LMB16 was done by referring to the original description of *Yunodorylus doryloides* of which the holotype was also collected in Sarawak, Malaysia (Bako National Park, near Kuching, rainforest, soil core, IV 1978, N. M. Collins). The following specimens and images of the type material were examined in the present study.

Yunodorylus doryloides (Borowiec, 2009): SFDC; 1 subdichthadiigyne (colony no. RS-55-LMB16; individual no. SEMUT20170111B); MALAYSIA, Sarawak, Miri, Lambir Hills National Park, 04°11'43.7"N 114°02'22.7"E, ca. 61 m alt., nr. Small lake; R. Satria leg.; 11.IX.2016. – SFDC; 7 workers (colony no. RS-55-LMB16; individual no. SEMUT20170907A. – SEMUT20170907G); same data with the subdichthadiigyne. – MHNG; 3 workers (colony no. RS-55-LMB16; individual no. SEMUT20170907H. – SEMUT20170907J); same data with the subdichthadiigyne.

Yunodorylus eguchii (Borowiec, 2009): MHNG; 1 subdichthadiigyne (colony no. Eg20ix15-01; individual no. IMG20160315-1); VIETNAM, Tay Ninh Province, Lo Go Xa Mat National Park, 11°35'17"N 105°53'01-10"E, ca. 5-15 m alt.; K. Eguchi leg.; 20.IX.2015.

Acanthostichus quadratus Emery, 1895: Images of the paralectotype queen (CASENT0903813) provided in AntWeb v7.2.9 (https://www.antweb.org/).

Ooceraea crypta (Mann, 1921): Images of the type material (USNM ENT 00529135) provided in the website of Smithsonian National Museum of Natural History (https://www.si.edu/).

Multi-focused montage images were produced using Helicon Focus Pro. (Helicon Soft Ltd., http://www.heliconsoft.com/) from a series of source images taken by a Panasonic Lumix DMC-GX8 digital camera attached to a Nikon AZ100 stereomicroscope. Artifacts/ghosts and unnecessary parts (unfocused appendages, insect pin, etc.) surrounding or covering target objects were erased and cleaned up using the retouching function of Helicon Focus Pro, and the color balance, contrast and sharpness were adjusted using Adobe Photoshop CS6.

The following parts of the bodies were measured using ImageJ 1.49m (National Institute of mental Health, USA, available at http://imageJ.nih.gov/ij/) based on the photographs taken using a Panasonic Lumix DMC-GX8 digital camera attached to the Nikon AZ100 stereomicroscope. Measurements and indices are modified from Eguchi *et al.* (2016). HL, maximum length of head in full-face view, measured from the midpoint of a line drawn across the anteriormost points of clypeus to the midpoint of a line drawn across posteriormost points of vertexal lobes of head; HW, maximum width of head in full-face view; SL, maximum length of antennal scape excluding the basal condylar bulb; ML, mesosomal length in dorsal view measured from the midpoint of anterior margin of promesonotal dome to the midpoint of a transverse line spanning the posterolateralmost points of mesosoma; MH, mesosoma height in lateral view measured from the lowermost point of mesopleuron (in front of middle coxa) to highest point of the dorsal outline of mesonotum; PNW, maximum width of pronotum; HFL, length of hind femur; MFL, length of mid femur; PH, maximum height of petiole (abdominal segment II) measured from an imaginary line of ventralmost point of petiole to the apex as measured in lateral view; PL, maximum diagonal length of petiole measured from the anteriormost point of the base of subpetiolar process to the posterodorsal corner of petiole; PW, maximum width of petiolar node; A3W, maximum width of abdominal segment III (gastral tergite I); A3L, maximum length of abdominal segment III (excluding helcium) in dorsal view: CI=HW/HLx100; SI=SL/HWx100; MI=WL/PNWx100; MFI=MFL/HWx100; A3I=A3W/PWx100; PTHI=PTH/PTLx100.

RESULTS AND DISCUSSION

Subdichthadiigyne of *Yunodorylus Doryloides*

Description (Figs 1-4): Head in full-face view subrectangular, longer than broad, with lateral outline straight parallel, with posterior margin broadly and strongly concave (Fig. 2A); head in lateral view with dorsal outline straight and ventral outline strongly convex; preoccipital carina absent; frontal lobes present as narrow erect to suberect walls, narrowly separated from each other by a longitudinal strip of median portion of clypeus (Fig. 2A); anteriormost portion of frontal lobe extending anteriad far beyond the anterior margin of clypeus (red arrow in Fig. 2A); parafrontal ridges completely absent; antennal socket in full-face view fully exposed, very close to anterior margin of head; clypeus narrow from front to back, with a straight anteromedian margin; lateroclypeal teeth low and rounded (blue arrow in Fig. 2A); mandible elongate and slender, with a large apical tooth followed by two small teeth on the masticatory margin; the edge behind the basalmost tooth of the masticatory margin almost straight (blue arrow in Fig. 3B); antenna 12-segmented; segment II longer than broad; segment III to XI broader than long; apical segment bullet-shaped with blunt apex, much longer than broad; compound eye absent; median and left lateral ocelli vestigial, recognized as small swellings, and right lateral ocellus completely absent (Fig. 2A); palp formula unknown (not dissected); mesosoma almost box-shaped, slightly slender, in lateral view with dorsal margin slightly convex, in dorsal view slightly constricted in front of propodeum, without flight sclerites; promesonotal suture faintly recognized, convex anteriad; metanotal groove faintly recognized, accompanied with a median small

Fig. 1. Subdichthadiigyne of *Yunodorylus doryloides* (colony no. RS-55-LMB16; individual no. SEMUT20170111B), body in lateral view.

depression (blue arrow in Fig. 2C); mesosoma in dorsal view distinctly longer than broad; anterior margin of mesopleuron weakly convex, but not forming a distinct lobe (red arrow in Fig. 2D); metapleural gland orifice concealed beneath a ventrolaterally directed cuticular flange; propodeum with a pair of faintly and bluntly produced posterodorsolateral corners, in posterodorsal view with a faint median longitudinal depression; an endophragmal pit distinct on the lateral face of propodeum (blue arrow in Fig. 2D); propodeal lobe very low; mesotibia and metatibia with a small simple spur in front of a large pectinate spurs; inner margin of pretarsal claws of all legs without teeth; metatibial gland absent; waist consisting of a single small segment (petiole); petiole without tergosternal fusion, in dorsal view much broader than long, broadest a little behind midlength of petiole, with anterior margin weakly concave and lateral margins weakly convex; subpetiolar process developed as a rectangular lobe, with an obtuse anteroventral and posteroventral angle (Fig. 4A); abdominal segments III–VII without tergosternal fusion; abdominal segment III with anterodorsal face (above helcium) vertical, with anteroventral face (below helcium) weakly humped; the anteroventral face without any margin or carina; pygidium convex, but not flattened nor impressed dorsally, apically without any specialized setae (such as thick and truncate-tipped setae), and without any peg-like or spine-like setae on posterolateral margins (Figs 4D, 4E); hypopygium flattened ventrally, with a U-shaped posterior margin, without any peg-like or spine-like setae on posterolateral margins (Fig. 4E); sting developed (Figs 4C, 4D, 4E).

Body densely covered with short standing hairs, less sculptured but densely with hair pits, yellowish-brown (see Fig. 1).

Measurements of the queen: HL 0.9 mm; HW 0.85 mm; SL 0.35 mm; ML 1.46 mm; MH 0.53 mm; PNW 0.61 mm;

Fig. 2. Subdichthadiigyne of *Yunodorylus doryloides* (colony no. RS-55-LMB16; individual no. SEMUT20170111B). (A) Head in full-face view, with a blue arrow indicating lateroclypeal tooth, and a red arrow indicating the anteriormost portion of frontal lobe. (B) Head in lateral view. (C) Mesosoma in dorsal view, with a blue arrow indicating median small depression. (D) Mesosoma in lateral view, with a blue arrow indicating an endophragmal pit, and red arrow indicating the anterior margin of mesopleuron.

HFL 0.57 mm; MFL 0.51 mm; PH 0.59 mm; PL 0.61 mm; PW 0.54 mm; A3W 0.80 mm; A3L 0.51 mm; CI 94.44; SI 41.18; MI 239.34; MFI 60; A3I 148.15.

Taxonomic remarks: The subdichthadiigyne of *Yunodorylus doryloides* is very similar to that of *Y. eguchii*. However, the following morphological differences were observed externally: mandible elongate and slender, with the edge behind the basalmost tooth of the masticatory margin almost straight in the former (blue arrow in Fig. 3B), but triangular, with the edge behind the basalmost tooth distinctly convex in the latter (red arrow in Fig. 3A); lateroclypeal teeth rounded in the former, but weakly pointed in the latter; mesosoma in dorsal view slenderer in the former than in the latter; mesonotum in dorsal view distinctly longer than broad in the former, but almost as long as broad in the latter; anterior margin of mesopleuron without a small lobe (red arrow in Fig. 2D) in the former, but with a small distinct lobe projecting over basal part of forecoxa

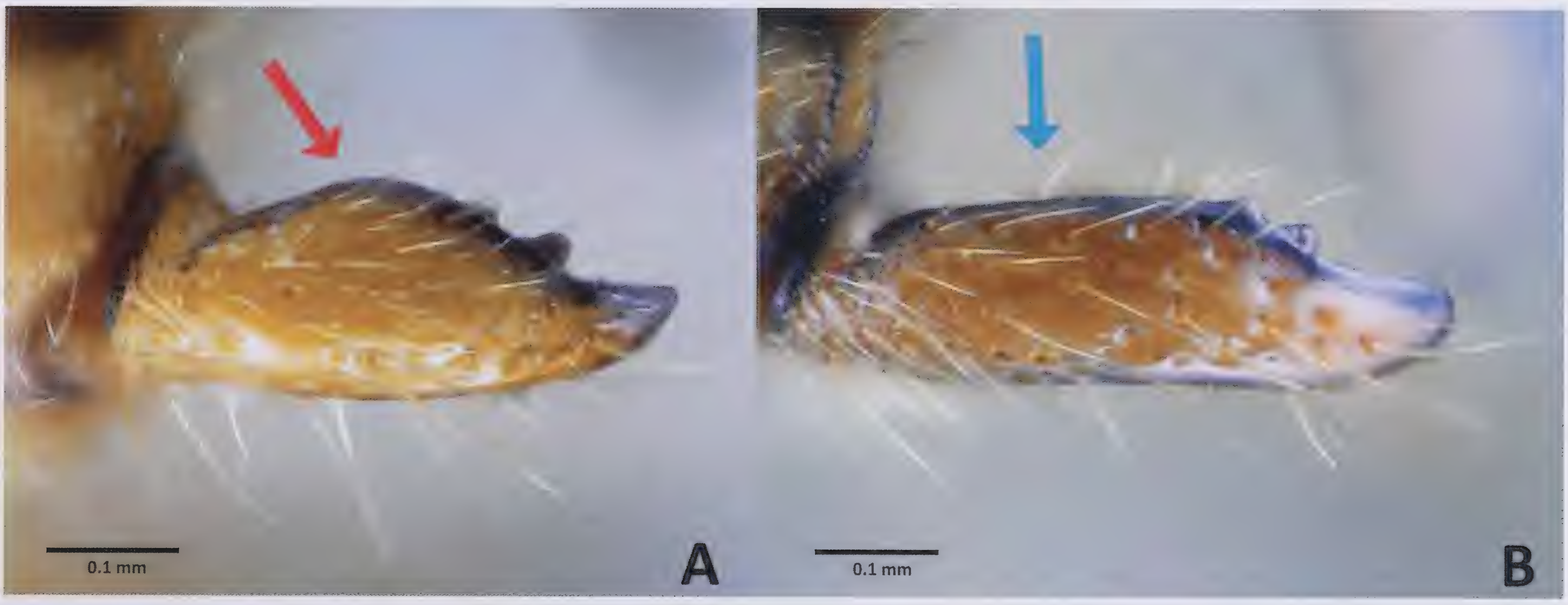

Fig. 3. Subdichthadiigyne of the genus *Yunodorylus,* mandible in full-face view with an arrow indicating edge of behind the basalmost tooth. (A) *Yunodorylus eguchii* (colony no. Eg20ix15-01; individual no. IMG20160315-1). (B) *Yunodorylus doryloides* (colony no. RS-55-LMB16; individual no. SEMUT20170111B).

in the latter; metanotal groove in dorsal view faintly recognized in the former, but relatively conspicuously recognized in the latter; ventral margin of metapleuron almost straight in the former, but weakly convex in the latter; petiole in dorsal view narrower and longer in the former than in the latter; pygidium apically without any specialized setae in the former, but with long, thick and truncate-tipped setae in the latter.

Eguchi *et al.* (2016) concluded that the queen of *Y. eguchii* is subdichthadiiform, because the worker-queen dimorphism is weaker in *Yunodorylus* than in the dorylomorph lineages with a full dichthadiigyne, i.e., the remarkable differences between the worker and queen in *Yunodorylus* are the body proportion, presence (worker) or absence (queen) of metatibial gland, and presence (worker) or absence (queen) of pygidial peg-like or spine-like setae. The present study on *Y. doryloides* also supported this view. The mode and degree of the morphological specialization in the subdichthadiigyne is similar among *Yunodorylus*, *Acanthostichus* (but a minority of the species has subdichthadiigynes), and *Ooceraea crypta*. However, interestingly, the "dichthadiigyne" of *O. crypta* has reduced compound eyes and three well-developed ocelli despite the worker lacking all of them (Borowiec, 2016). The visual function is presumably related to the mode of colony moving.

Biological remarks: The colony was found in soft and clayish soil under a rotting log on the floor of the forest edge near a natural pond. Although colonies of *Y. eguchii* were found in thick soil walls of termite mounds built on the ground of lowland evergreen forest (Eguchi *et al.*, 2016), no relationship with termites was observed for *Y. doryloides*. The colony consisted of a single subdichthadiigyne, 393 workers, and 237 tiny larvae in earlier instar only. This suggests the presence of synchronized brood development in *Y. doryloides* as expected in *Y. eguchii* (Eguchi *et al.*, 2016).

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REFERENCES

Bolton B. 2003. Synopsis and Classification of Formicidae. *Memoirs of the American Entomological Institute* 71: 370 pp.

Borowiec M.L. 2009. New species related to *Cerapachys sexspinus* and discussion of the status of *Yunodorylus*. *Zootaxa* 2069: 43-58.

Borowiec M.L. 2016. Generic revision of the ant subfamily

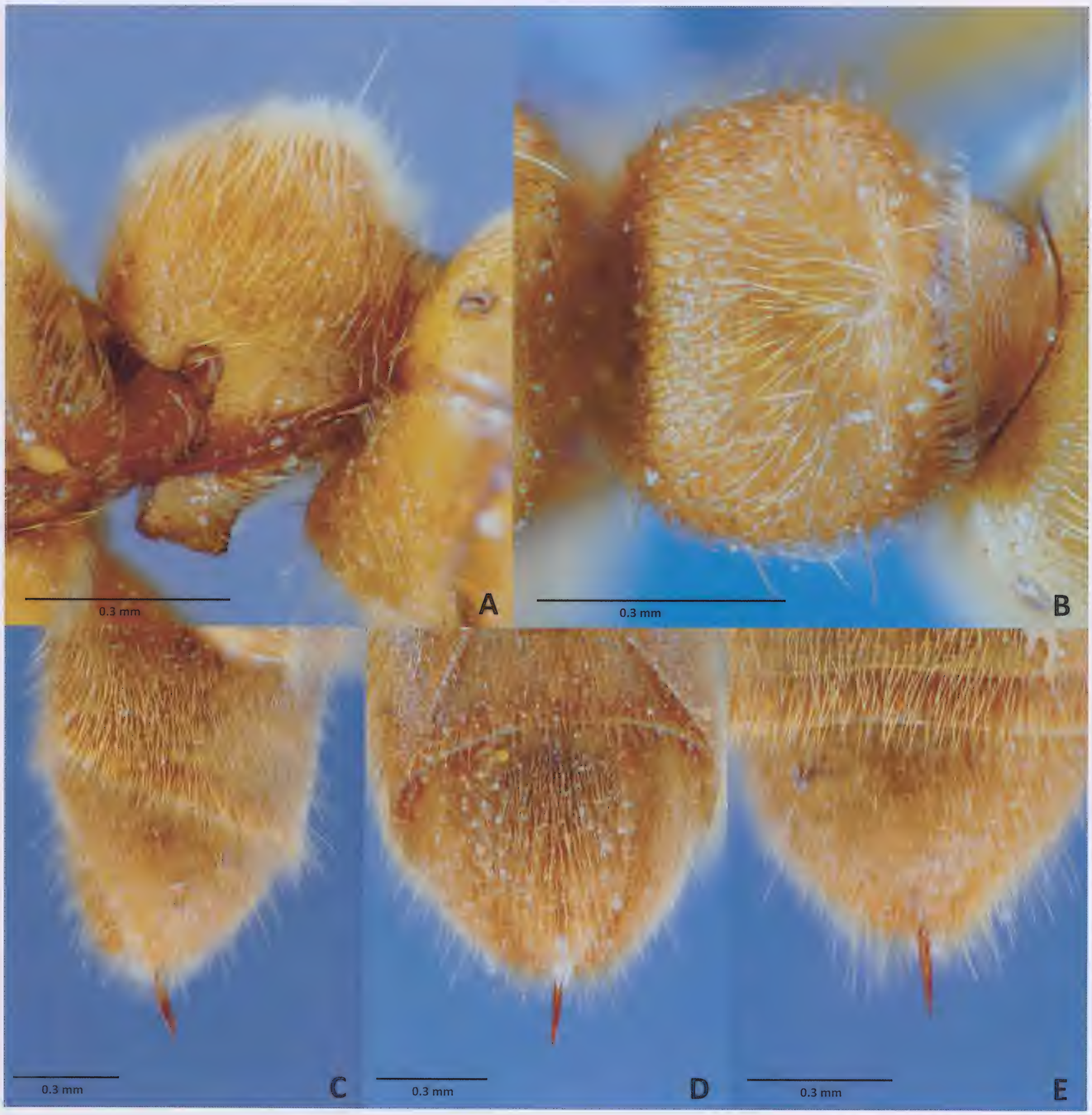

Fig. 4. Subdichthadiigyne of *Yunodorylus doryloides* (colony no. RS-55-LMB16; individual no. SEMUT20170111B). (A) Petiole in lateral view. (B) Petiole in dorsal view. (C) Apex of gaster in lateral view. (D) Hypopygium in ventral view. (E) Pygidium in dorsal view.

Dorylinae (Hymenoptera, Formicidae). *ZooKeys* 608: 1-280.

Brady S.G., Fisher B.L., Schultz T.R., Ward P. S. 2014. The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evolutionary Biology*, 2014, 14: 93, 14 pp. https://DOI.org/10.1186/1471-2148-14-93

Eguchi K., Mizuno R., Ito F., Satria R., Dang V.A., Bui T.V., Phung T.H.L. 2016. First discovery of subdichthadiigyne in *Yunodorylus* Xu, 2000 (Formicidae: Dorylinae). *Revue suisse de Zoologie* 123: 307-314. https://DOI.org/10.5281/zenodo.155307

Emery C. 1895. Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 8: 685-677.

Mann W.M. 1921. The ants of the Fiji Islands. *Bulletin of the Museum of Comparative Zoology* 64: 401-499.

Smith F. 1857. Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A. R. Wallace. *Journal and Proceedings of the Linnean Society of London, Zoology* 2: 42-88.

Xu Z.H. 2000. Two new genera of ant subfamilies Dorylinae and Ponerinae (Hymenoptera: Formicidae) from Yunnan, China. *Zoological Research* 21: 297-302.

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New data on the genus *Pycnoscelus* Scudder, 1862 with the description of *P. schwendingeri* sp. nov. (Blaberidae: Pycnoscelinae)

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Abstract: A new species of cockroach, *Pycnoscelus schwendingeri* sp. nov., is reported from Cambodia. A detailed morphological description of the new species is given. *Pycnoscelus surinamensis* and *P. striatus* are redescribed. The structure of the female genital complex, i.e. anal and genital plates, ovipositor and adjacent structures, of *Pycnoscelus surinamensis* and the male genitalia of *P. striatus* are redescribed in detail.

Keywords: *Pycnoscelus surinamensis* - *Pycnoscelus striatus* - morphology.

INTRODUCTION

The genus *Pycnoscelus* Scudder, 1862 includes highly specialized cockroaches with more or less pronounced adaptations to living in litter and digging. The genus was reviewed by Roth (1973, 1998). New information on this genus was recently added by Anisyutkin (2002, 2004) and by Lucañas & Lit (2016). In the present paper a new species, *Pycnoscelus schwendingeri* sp. nov., is described and new data on *Pycnoscelus* morphology are given.

MATERIAL AND METHODS

The author generally follows methods described earlier (Anisyutkin, 2014, 2015). Rehn's (1951) terminology of tegmina and wing venation is used. The description of the anterior margin of the fore femur armament follows Bey-Bienko (1950) and Roth (2003). The terminology of male genital sclerites follows Klass (1997), with some modifications. The terminology used by Grandcolas (1996) for genital structures is given in parentheses. Terminology of female genital structures follows McKittrick (1964) and Klass (1998). Terms introduced by the author (in the present work and in Anisyutkin, 2014, 2015) are given in quotation marks.

The material examined has been deposited in the Muséum d'histoire naturelle in Geneva (MHNG) and in the Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg, Russia (ZIN).

Abbreviation used in figures
(See text for further details):

a.a.	anterior arch of second valvifer of female genitalia;
ap.scl.	"apical sclerite" of sclerite L2D in male genitalia;
b.L2D	basal part of sclerite L2D in male genitalia;
b.L3	basal subsclerite of sclerite L3 in male genitalia;
bsv.	basivalvula of female genitalia;
c.p.R1T	caudal part of sclerite R1T in male genitalia;
Cer.	cercus;
CuP	second cubital, "cubitus posterior", vein of tegmina;
d.o.	"dorsal outgrows" of apical part of sclerite L2D in male genitalia;
f.s.	"folded structure" of sclerite L3 in male genitalia;
gg.	gonangulum of female genitalia;
h.	hook at right posterolateral angle of hypandrium;
hge	groove of sclerite L3 in male genitalia (sensu Klass, 1997);
IX	9th abdominal tergite;
L2D, L3, L4U	sclerites in male genitalia;
L2d, L3d	sclerites in male genitalia according to Grandcolas (1996);
M	medial vein of tegmina;

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par.	paraproct;
pl.	sclerotized lobes of 2nd and 3rd pairs of valves in female genitalia;
R	radial vein of tegmina;
R+N	sclerites in male genitalia according to Grandcolas (1996);
R1T, R2, R3, R4, R5	sclerites in male genitalia;
s.t.	"small tooth" of apical part of sclerite L3 in male genitalia;
Sc	costal vein of tegmina;
teVIII.	tergal process of 8th abdominal tergite;
teIX.	tergal process of 9th abdominal tergite;
v.I., v.II., v.III.	1st, 2nd and 3rd valves of ovipositor;
vs.	vestibular sclerite in female genitalia;
X	10th abdominal tergite.

TAXONOMIC PART

Genus *Pycnoscelus* Scudder, 1862

Type species: *Pycnoscelus obscurus* Scudder, 1862 [= *P. surinamensis* (Linnaeus, 1758)], by monotypy.

Remarks: The genus was described as monotypical, on the basis of a single specimen that Scudder (1862) believed to be a male. However, it is evident from the original description that this specimen is actually a larva. Later, *P. obscurus* was synonymized with *P. surinamensis* by Princis (1964).

Pycnoscelus surinamensis is a parthenogenetic (thelytokous) species with a worldwide distribution. The closely related *P. indicus* is a bisexual species distributed in South and South-East Asia (Roth, 1998). *Pycnoscelus indicus* is evidently most closely related to *P. surinamensis*. I previously considered these as parthenogenetic and bisexual forms of a single species (Anisyutkin, 2002), but meanwhile I changed my view and follow Roth (1967, 1974, 1998) in regarding them as two distinct species: *P. indicus* and *P. surinamensis*.

Species included: Those given in Beccaloni (2014) [*P. aurantia* Hanitsch, 1935, *P. conferta* Walker, 1869, *P. femapterus* Roth, 1998, *P. gorochovi* Anisyutkin, 2002, *P. indicus* (Fabricius, 1775), *P. janetscheki* Bey-Bienko, 1968, *P. micropterus* Hanitsch, 1931, *P. nigra* (Brunner von Wattenwyl, 1865), *P. rothi* Anisyutkin, 2002, *P. semivitreus* Princis, 1967, *P. striatus* (Kirby, 1903), *P. surinamensis* (Linnaeus, 1758), *P. tenebrigera* (Walker, 1868) and *P. vietnamensis* Anisyutkin, 2002] plus *P. schwendingeri* sp. nov.

Pycnoscelus surinamensis (Linnaeus, 1758)
Figs 1-5

Material examined: ZIN, without accession number; 5 females of unknown provenance, reared in captivity in Saint Petersburg in 2017.

Additions to description of female (Figs 1-5): Based on specimens listed above, the description of Roth (1998) can be supplemented with the following details.

Somatic characters of female (Figs 1-2): Abdomen without visible glandular specializations; spiracle-bearing outgrowths of tergite VIII weakly expressed (Fig. 1). Anal plate (tergite X) wider than long, its hind margin widely rounded and with a weak medial notch (Fig. 1). Cerci short, flatten, with segments solidly connected but distinct (Fig. 1). Genital plate wide, with a distinct pair of paramedian emarginations on hind margin (Fig. 2). Paraprocts mostly membranous, bordered with a thin angulate sclerite on anterior and posterior side (Fig. 3, *par.*).

Ovipositor and adjacent structures (Figs 3-5): Intercalary sclerite absent. Tergal processes of abdominal segment VIII wide and reduced, not reaching paratergites of tergite VIII, fused with basivalvula (Fig. 3, *teVIII.*); tergal processes of abdominal segment IX fully developed (Fig. 3, *teIX.*). Gonangulum distinct, well sclerotized (Figs 3-5, *gg.*). All valves of ovipositor mostly membranous, only partly sclerotized. First valves large, membranous at apex, with numerous setae along inner side (Fig. 4, *v.I.*). Base of 2nd and 3rd pairs of valves as in Fig. 5, sclerotized lobes well developed (Figs 4-5, *pl.*). Anterior arch of second valvifer slightly angulate, as in Fig. 5, *a.a.* Second valves of ovipositor small, completely hidden under 1st ones (Fig. 4, *v.II.*). Third valves of ovipositor (gonoplacs) wide (Figs 3-4, *v.III.*). Basivalvula developed as a pair of slightly asymmetrical, widely rounded and partly sclerotized plates (Figs 3-5, *bsv.*). Vestibular structure in shape of membranous pad (Fig. 3, *vs.*). Brood sac (Fig. 3) without sclerotized structures.

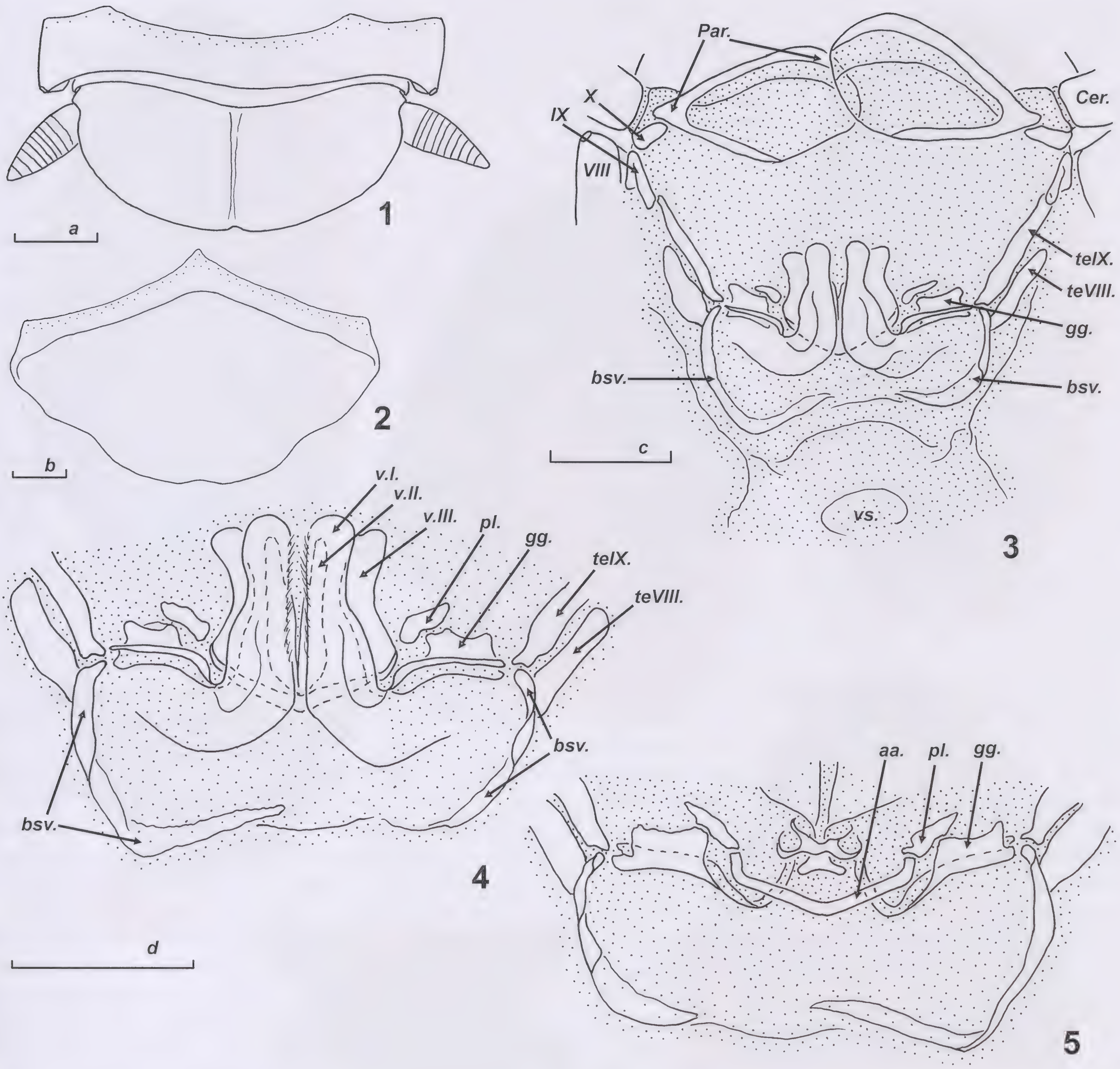
Pycnoscelus schwendingeri sp. nov.
Figs 6-7, 12-26

Material examined: MHNG, without accession number; male holotype (genital complex in prep. 110817/01); THKN-12/04: Cambodia, Siem Reap Prov., Kbal Spean (13°41'04"N, 104°01'10"E), 200 m, semi-evergreen forest; 27.VI.2013; leg. P. Schwendinger.

Etymology: This species is named in honor of Dr Peter Schwendinger, collector of the holotype of this species and curator of the Arthropoda collections of the Muséum d'histoire naturelle de Genève.

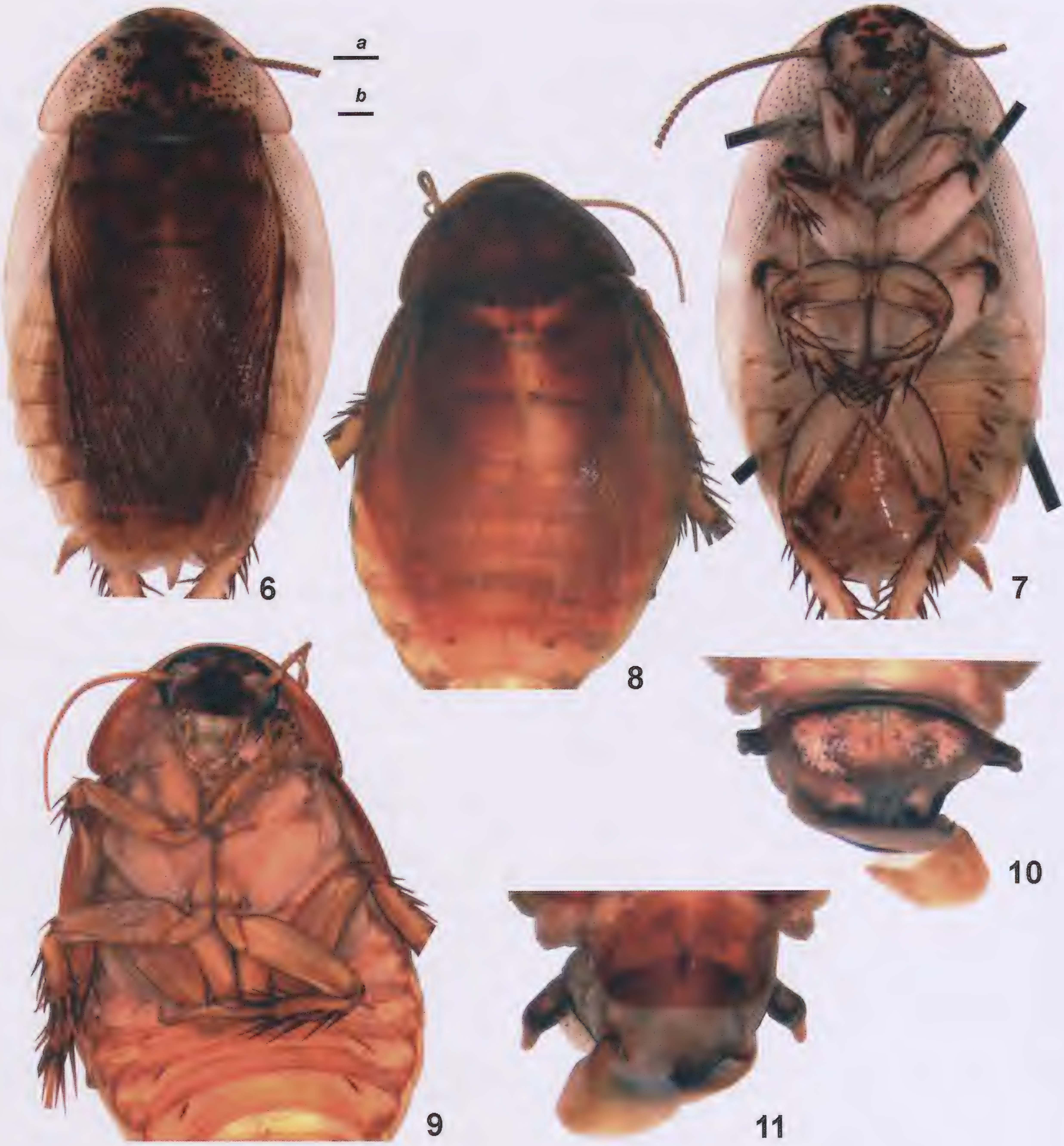
Description:

Somatic characters of male (holotype): General colour yellowish brown, with scattered black spots (Figs 6-7);



Figs 1-5. *Pycnoscelus surinamensis* (Linnaeus, 1758), female. (1) Abdominal apex, dorsal view. (2) Genital plate, ventral view. (3) Ovipositor and adjacent structures, ventral view. (4) Ovipositor, ventral view. (5) Basal part of ovipositor, dorsal view. Dotted areas show membranous parts, except for valves of ovipositor in Figs 3-4. Abbreviations: *aa.*, *bsv.*, *Cer.*, *gg.*, *par.*, *pl.*, *teVIII.*, *teIX.*, *v.I.*, *v.II.*, *v.III.*, *vs.* - see paragraph "abbreviation used in figures"; *VIII*, *IX*, *X* - abdominal tergites VIII-X; for details see text. Scale bars 1 mm: a: 1, b: 2, c: 3, d: 4-5.

facial part of head contrastingly coloured (Fig. 7); eyes black; antennae greyish; pronotum, tegmina and abdominal sternites with black spots; legs yellow, partly darkened. Surfaces smooth and lustrous, antennae with proximal 8-10 segments lustrous, the remaining segments dull; pronotum, tegmina, mostly in proximal half, and, to a lesser degree, facial part of head with distinct punctuation. Head slightly longer than wide, with transverse impression between antennal sockets (Figs 7, 12); ocellar spots small but distinct; distance between eyes about equal to eye length; distance between antennal sockets about 2.5 times scape length (~0.6 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.1 : 1.0 : 1.2. Pronotum as in Figs 6, 13; cranial margin widely rounded, caudal one distinctly angulate. Tegmina and wings slightly abbreviate, reaching abdominal apex (Figs 6-7). Tegmina with widely rounded apex (Fig. 6), sclerotized in costal field; venation simplified and slightly obliterated along cranial margin; *Sc* thickened (well visible on ventral side of tegmen); *R*, *M* and *CuP* weak; anal field with obliterated venation. Hind wings membranous, shorter



Figs 6-11. Photos of males of *Pycnoscelus schwendingeri* sp. nov. (6-7: holotype) and *P. striatus* (Kirby, 1903) (8-11: specimen from Batu Caves). (6, 8) General view from above. (7, 9) General view from below. (10) Abdominal apex, dorsal view. (11) Same, ventral view. Stylus in Figs 10-11 in everted state. Scale bars 10 mm: a: 6, b: 8. Other photos not to scale.

than tegmina, with simplified venation. Fore tibiae distinctly thickened distally (Fig. 14). Anterior margin of fore femora of armed type C, with single apical spine (Fig. 14). Tibial spines well developed. Structure of hind tarsus (Fig. 15): metatarsus about as long as other tarsal segments combined, with large euplantula; spines absent; claws symmetrical, simple; arolium distinct, about half as long as claw. Fore and mid tarsi similar to hind tarsi, but segments comparatively shorter. Abdomen without visible glandular specializations; tergite VIII with distinct spiracle-bearing outgrowths (Figs 16-17), large medial and two smaller oval lateral membranous areas; sternite VIII large, plate-like and weakly sclerotized (Fig. 18). Anal plate (tergite X) weakly sclerotized and asymmetrical (Figs 16-17). Cerci short, with distinct segments. Paraprocts of blaberi-type, with curved

hook on right paraproct and with membranous area at cranio-medial angles of left paraproct (Fig. 17, *par.*). Hypandrium asymmetrical (Figs 19-20), with caudal margin weakly concave, hook at caudolateral angle well sclerotized (Fig. 20, *h.*); left stylus absent, right one in shape of elongated triangle.

Genitalia of male holotype (Figs 20-26): Right phallomere (*R+N*): caudal part of sclerite *R1T* well sclerotized, widely rounded (Fig. 21, *c.p.R1T*); bristles absent; *R1T* nearly straight; *R2* weakly curved; *R3* elongated (Figs 21-22); *R4* small, not fused with other sclerites; *R5* absent; *R1T* and *R2* cranially prolonged into large sclerotized plate. Sclerite *L2D* (*L1*) divided into basal and apical parts (Fig. 24); basal part robust, widened cranially (Fig. 24, *b.L2D*); "apical sclerite" with small teeth at caudal margin (Figs 23-24, *ap. scl.*); bristles absent; "dorsal outgrowth" present (Figs 23-24, *d.o.*). Sclerite *L3* (*L2d*) without basal subsclerite (Figs 25-26); "folded structure" weakly developed, without bristles (Fig. 26, *f.s.*); apex of *L3* with "small tooth" (Figs 25-26, *s.t.*); groove *hge* absent. Sclerite *L4U* (*L3d*) divided into two parts (Fig. 25).

Female: Unknown.

Measurements (in mm): Head length 2.6, head width 2.5; pronotum length 4.0, pronotum width 5.8; tegmen length 10.8, tegmen width 3.9.

Comparison: *Pycnoscelus schwendingeri* sp. nov. belongs to the *indicus* species-group (Roth, 1998) judging from the structure of its right stylus. This species-group includes nine species (Roth, 1998; Anisyutkin, 2002): *P. conferta*, *P. femapterus*, *P. indicus*, *P. janetcheki*, *P. nigra*, *P. surinamensis*, *P. gorochovi*, *P. vietnamensis* and *P. rothi*. The new species readily differs from all species of the *indicus* species-group by a contrastingly coloured pronotum and facial part of head (Figs 6-7). From *P. indicus*, *P. nigra*, *P. janetsheki*, *P. conferta* and *P. femapterus* the new species differs by a distinctly asymmetrical, i.e. emarginated at right side (Figs 16-17), anal plate. The shape of the anal plate is somewhat similar in *P. gorochovi*, *P. vietnamensis*, *P. rothi* and *P. schwendingeri* sp. nov., but these species can be readily differentiated by the shape of the apical part of sclerite *L2D* of the male genitalia (compare figs 26-28 in Anisyutkin, 2002 and Figs 23-24 of present paper).

Pycnoscelus striatus (Kirby, 1903)

Figs 8-11, 27-38

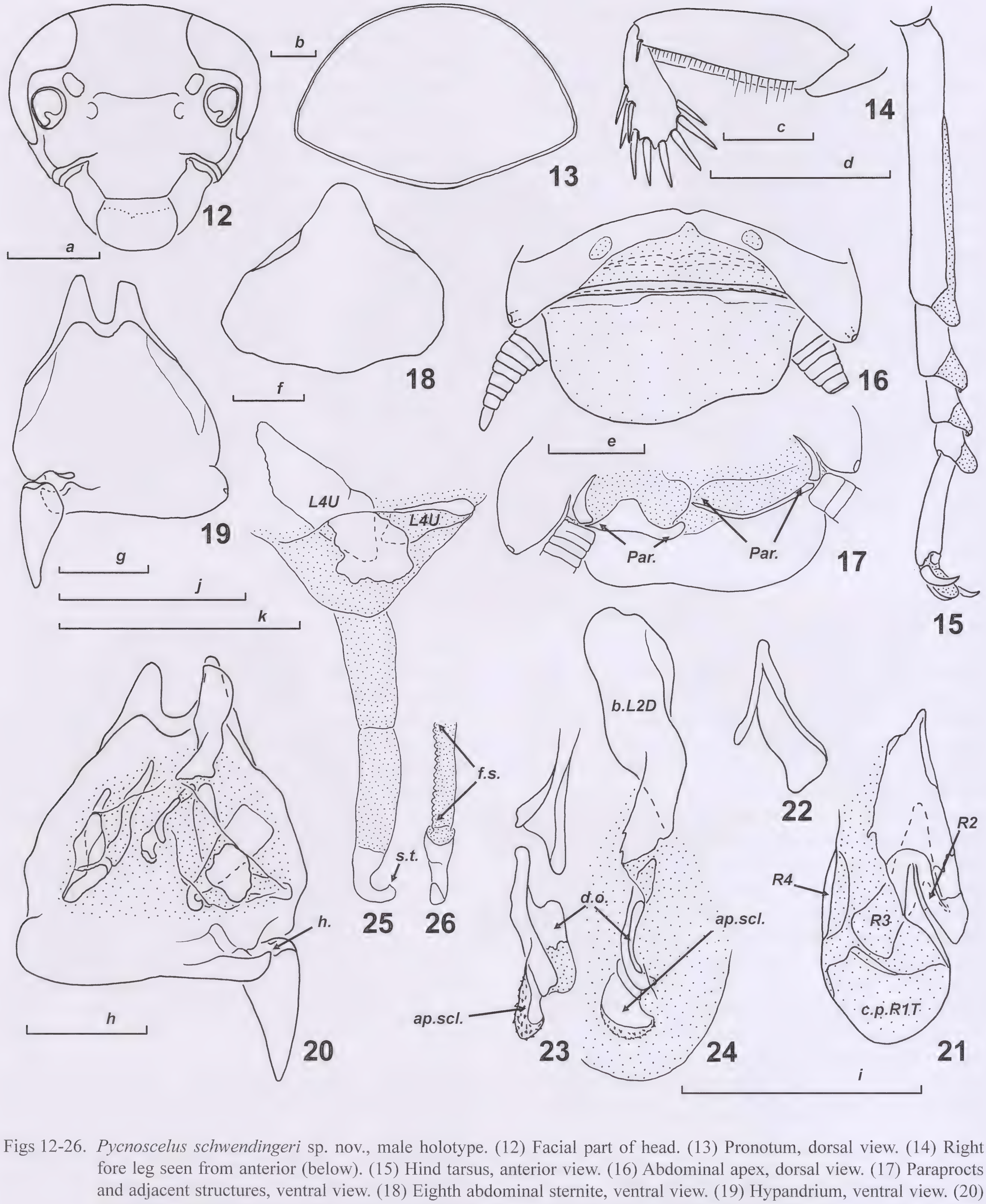
Material examined: MHNG, without accession number; 1 male (genital complex in prep. 110817/02) and 18 larvae; W. Malaysia, N. of Kuala-Lumpur, Batu Caves; November 1976; collector unknown, probably Dr Brigitte Köpchen.

Description: On the basis of the newly examined male specimen the description of Roth (1998) can be supplemented with the following details.

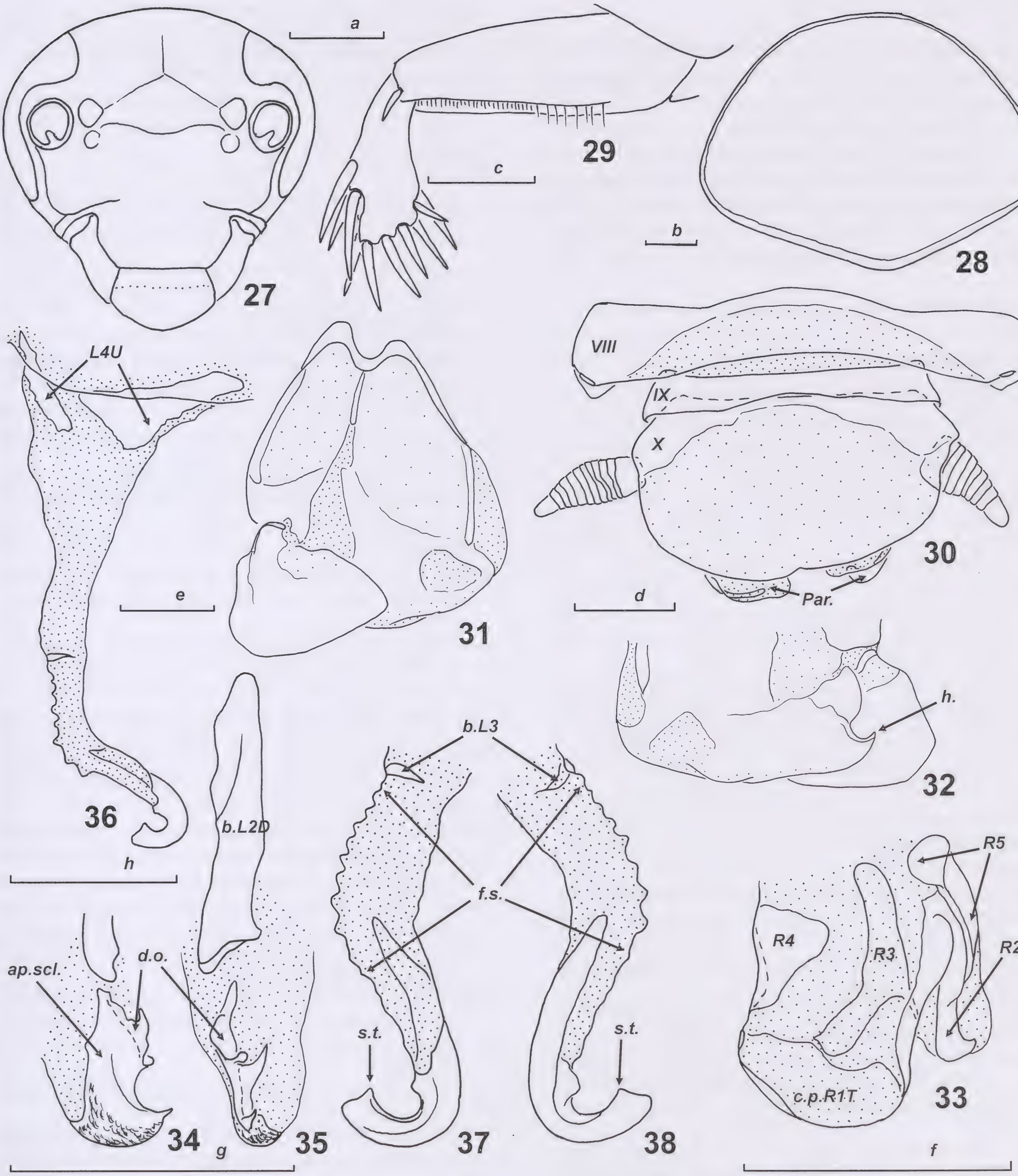
Somatic characters of male: General colour yellowish brown (Figs 8-11), pronotum and facial part of head darker; eyes black. Surfaces smooth and lustrous, antennae with lustrous proximal 6-7 segments, remaining segments dull; pronotum and tegmina, mostly in proximal half, with distinct punctuation. Head as in Figs 9, 27, slightly longer than wide, with transverse impression between antennal sockets; ocellar spots small but distinct; distance between eyes about equal to eye length; distance between antennal sockets about 2.5 times scape length (~0.6 mm); approximate length ratio of 3rd-5th segments of maxillary palps 1.3 : 1.0 : 1.3. Pronotum as in Figs 8, 28. Tegmina and hind wings distinctly abbreviate, not reaching abdominal apex. Fore tibiae distinctly thickened distally (Fig. 29). Anterior margin of fore femora of armed type C, with single apical spine (Fig. 29). Tibial spines well developed. Structure of hind tarsus similar to that of *P. schwendingeri* sp. nov., but metatarsus slightly longer than other segments combined, distally bordered with pair of "additional spines"; 2nd and 3rd tarsal segments with "additional spines" on their outside; arolium distinct, smaller than one half of claw length. Fore and mid tarsi similar to hind tarsi, but segments comparatively shorter. Abdomen without visible glandular specializations; tergite VIII with distinct spiracle-bearing outgrowths (Figs 10-11, 30) and large medial membranous area; sternite VIII large, plate-like. Anal plate (tergite X) weakly sclerotized, very weakly asymmetrical (Figs 10, 30). Cerci short, with distinct segments (Figs 10, 30). Paraprocts of blaberi-type, similar to those of *P. schwendingeri* sp. nov. Hypandrium asymmetrical, irregularly sclerotized (Figs 11, 31-32), with caudal margin convex, hook at posterolateral angle well sclerotized (Fig. 32, *h.*); left stylus absent, right one in shape of wide plate.

Male genitalia (Figs 33-38): Right phallomere (*R+N*): caudal part of sclerite *R1T* well sclerotized, widely rounded (Fig. 33, *c.p.R1T*); bristles absent; *R1T* nearly straight; *R2* weakly curved; *R3* elongated, similar to that of *P. schwendingeri* sp. nov.; *R4* plate-like, not fused with other sclerites; *R5* elongated. Sclerite *L2D* (*L1*) divided into basal and apical parts (Fig. 35); basal part robust (Fig. 35, *b.L2D*); "apical sclerite" with recumbent bristles (Figs 34-35, *ap. scl.*); "dorsal outgrowth" weak (Figs 34-35, *d.o.*). Sclerite *L3* (*L2d*) with basal subsclerite (Figs 36-38, *b.L3*); "folded structure" present, without bristles (Figs 36-38, *f.s.*); apex of *L3* with "small tooth" (Figs 36-38, *s.t.*); groove *hge* absent. Sclerite *L4U* (*L3d*) divided into two parts (Fig. 36).

Measurements (in mm): Head length 3.4, head width 3.2; pronotum length 5.0, pronotum width 6.5; tegmen length 10.9, tegmen width 5.0.



Figs 12-26. *Pycnoscelus schwendingeri* sp. nov., male holotype. (12) Facial part of head. (13) Pronotum, dorsal view. (14) Right fore leg seen from anterior (below). (15) Hind tarsus, anterior view. (16) Abdominal apex, dorsal view. (17) Paraprocts and adjacent structures, ventral view. (18) Eighth abdominal sternite, ventral view. (19) Hypandrium, ventral view. (20) Hypandrium and genitalia, dorsal view. (21) Right phallomere, dorsal view. (22) Sclerite *R3*, ventral view. (23) Caudal part of sclerite *L2D*, lateral view. (24) Sclerite *L2D*, dorsal view. (25) Sclerites *L3* and *L4U*, dorsal view. (26) Apex of sclerite *L3*. Dotted areas show membranous parts. Abbreviations: *ap.scl.*, *b.L2D*, *c.p.R1T*, *d.o.*, *f.s.*, *h.*, *L4U*, *par.*, *R2*, *R3*, *R4*, *s.t.* - see paragraph "abbreviation used in figures"; for details see text. Scale bars 1 mm: a: 12, b: 13, c: 14, d: 15, e: 16-17, f: 18, g: 19, h: 20, i: 21-24, j: 25, k: 26.



Figs 27-38. *Pycnoscelus striatus* (Kirby, 1903), male from Batu Caves. (27) Facial part of head. (28) Pronotum, dorsal view. (29) Right fore leg seen from anterior (below). (30) Abdominal apex, dorsal view. (31) Hypandrium, ventral view. (32) Caudal part of hypandrium, dorsal view. (33) Right phallomere, dorsal view. (34) Caudal part of sclerite *L2D*, lateral view. (35) Sclerite *L2D*, dorsal view. (36) Sclerites *L3* and *L4U*, dorsal view. (37-38) Apex of sclerite *L3*. Dotted areas show membranous parts. Abbreviations: *ap.scl.*, *b.L2D*, *b.L3*, *c.p.R1T*, *d.o.*, *f.s.*, *h.*, *L4U*, *par.*, *R2*, *R3*, *R4*, *R5*, *s.t.* - see paragraph "abbreviation used in figures"; *VIII*, *IX*, *X* - abdominal tergites VIII-X; for details see text. Scale bars 1 mm: a: 27, b: 28, c: 29, d: 30, 32, e: 31, f: 33, g: 34-35, 37-38, h: 36.

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REFERENCES

Anisyutkin L.N. 2002. Notes on the cockroaches of the subfamily Pycnoscelinae and Diplopterinae from South-East Asia (Blaberidae: Dictyoptera). *Zoosystematica Rossica* (for 2001) 10(2): 351-359.

Anisyutkin L.N. 2004. Redescription of *Pycnoscelus rufus* Bey-Bienko, *Heminauphoeta picea* Shelford and *Euthe-ganopteryx mirabilis* Shelford (Dictyoptera: Blattina). *Zoosystematica Rossica* (for 2003) 12(2): 177-183.

Anisyutkin L.N. 2014. On cockroaches of the subfamily Epilamprinae (Dictyoptera: Blaberidae) from South India and Sri Lanka, with descriptions of new taxa. *Zootaxa* 3847(3): 301-332.

Anisyutkin L.N. 2015. New and little known known Epilamprinae (Dictyoptera: Blaberidae) from the collections of the Muséum d'histoire naturelle de Genève and the Zoological Institute of Saint Petersburg. Part 1. *Revue suisse de Zoologie* 122(2): 283-296.

Beccaloni G.W. 2014. Cockroach Species File Online. Version 5.0/5.0. World Wide Web electronic publication. Available at http://Cockroach.SpeciesFile.org (accessed 10 August 2017).

Bey-Bienko G.Y. 1950. Cockroach insects. *Fauna USSR* (New Series) 40: 1-343.

Bey-Bienko G.Y. 1968. On the orthopteroid insects (Orthopteroidea) from Eastern Nepal. *Entomologicheskoe Obozrenie* 48(1): 106-130.

Brunner von Wattenwyl C. 1865. Nouveau système des Blattaires. *Charles Ueberreuter, Wien*, 426 pp.

Fabricius J.C. 1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. *Korte, Flensburgi et Lipsiae*, 832 pp.

Grandcolas P. 1996. The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Canadian Journal of Zoology* 74(3): 508-527.

Hanitsch R. 1931. On a collection of Malayan Blattidae from the British Museum (Natural History). *Annals and Magazine of Natural History* (Series 10) 7: 385-408.

Hanitsch R. 1935. On further Blattids (Orth.) from Celebes. *Stylops* 4: 14-19.

Kirby W.F. 1903. Notes on Blattidae & c., with descriptions of new genera and species in the collection of the British Museum, South Kensington. III. *Annals and Magazine of Natural History* (Series 7) 12: 373-381.

Klass K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner Zoologische Monographien* 42: 1-341.

Klass K.-D. 1998. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. *Zoologischer Anzeiger* 236: 69-101.

Linnaeus C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio X, reformata. *Salvius*, *Holmiae*, 824 pp.

Lucañas C., Lit I.L. 2016. Cockroaches (Insecta, Blattodea) from caves of Polilo Island (Philippines), with description of a new species. *Subterranean Biology* 19: 51-64.

McKittrick F.A. 1964. Evolutionary studies of cockroaches. *Cornell University Agricultural Experiments Station Memoir* 389: 1-197.

Princis K. 1964. Blattariae: Subordo Blaberoidea. Fam.: Panchloridae, Gynopeltidae, Derocalymmidae, Perisphaeriidae, Pycnoscelididae. *Orthopterorum Catalogus* 6: 174-281.

Princis K. 1967. Kleine Beiträge zur Kenntnis der Blattarien und ihrer Verbreitung. X. *Opuscula entomologica* 32(1-2): 141-151.

Rehn J.W.H. 1951. Classification of the Blattaria as indicated by their wings (Orthoptera). *Memoirs of the American Entomological Society* 14: 1-134.

Roth L.M. 1967. Sexual isolation in parthenogenetic *Pycnoscelus surinamensis* and application of the name *Pycnoscelus indicus* to its bisexual relative (Dictyoptera: Blattaria: Blaberidae: Pycnoscelinae). *Annals of the Entomological Society of America* 60(4): 774-779.

Roth L.M. 1973. The male genitalia of Blattaria. X. Blaberidae. *Pycnoscelus*, *Stilpnoblatta*, *Proscratea* (Pycnoscelinae), and *Diploptera* (Diplopterinae). *Psyche* 80: 249-264.

Roth L.M. 1974. Reproductive potential of bisexual *Pycnoscelus indicus* and clones of its parthenogenetic relative, *Pycnoscelus surinamensis*. *Annals of the Entomological Society of America* 67(2): 215-223.

Roth L.M. 1998. The cockroach genus *Pycnoscelus* Scudder, with a description of *Pycnoscelus femapterus*, sp. nov. (Blattaria: Blaberidae: Pycnoscelinae). *Oriental Insects* 32: 93-130.

Roth L.M. 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects* 37: 1-186.

Scudder S.H. 1862. Materials for a monograph of the North American Orthoptera, including a catalogue of the known New England species. *Boston Journal of Natural History* 7: 409-480.

Walker F. 1868. Catalogue of the specimens of Blattariae in the collection of the British Museum. *British Museum, London*, 239 pp.

Walker F. 1869. Catalogue of the specimens of Dermaptera, Saltatoria and supplement to the Blattariae in the collection of the British Museum. *British Museum*, *London*, 224 pp.

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A survey of the genus *Nasoona* Locket, 1982 with the description of six new species (Araneae, Linyphiidae)

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Abstract: Taxonomic notes on the spider genus *Nasoona* Locket, 1982 are provided. Six species are described as new: *Nasoona indiana* sp. nov. (male) and *N. orissa* sp. nov. (male) from the Oriental part of India; *N. intuberosa* sp. nov. (male and female), *N. kinabalu* sp. nov. (male and female) and *N. sabah* sp. nov. (male and female) from Borneo, as well as *N. sulawesi* sp. nov. (male) from northern Sulawesi. The female of *N. comata* (Tanasevitch, 1998) from Nepal is described for the first time. *Nasoona nigromaculata* Gao, Fei & Xing, 1996 is transferred to *Oedothorax* Bertkau in Förster & Bertkau, 1883. New faunistic data on *N. comata* (Tanasevitch, 1998), *N. chrysanthusi* Locket, 1982, *N. crucifera* (Thorell, 1895) and *N. prominula* Locket, 1982 are given. The distribution of the genus can be characterized as disjunct Oriental-Neotropical.

Keywords: Erigoninae - India - East Malaysia - Indonesia - Southeast Asia.

INTRODUCTION

The spider spider genus *Nasoona* Locket, 1982 was erected by Locket (1982) for *N. prominula* Locket, 1982 (the type species) and *N. chrysanthusi* Locket, 1982, both described from the southern part of the Malay Peninsula, West Malaysia. Later the genus has been replenished with new species and species transferred here from other genera (Millidge, 1995; Gao *et al.*, 1996; Tanasevitch, 2014). Currently the genus comprises 12 species, distributed mainly in the Oriental Region (World Spider Catalog, 2017). Another six new species from India, East Malaysia and Indonesia are described below; one species is removed from the genus.

MATERIAL AND METHODS

This paper is based mainly on material kept at the Muséum d'histoire naturelle de Genève, Switzerland (MHNG), a few additional specimens were available from the Senckenberg Museum, Frankfurt am Main, Germany (SMF) and from the Zoological Museum of the Moscow State University, Moscow, Russia (ZMMU). If not mentioned otherwise, the material examined is deposited in the MHNG. Sample numbers are given in square brackets.

Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. A Levenhuk C-800 digital camera was used for photos. The terminology of copulatory organs mainly follows that of Merrett (1963), Hormiga (2000) and Tanasevitch (1998, 2014, 2015). The chaetotaxy is given in a formula, e.g., 2.2.1.1, which refers to the number of dorsal spines on tibiae I-IV. The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. All scale bars in the figures correspond to 0.1 mm.

Abbreviations

"A"	basal apophysis of the embolic division *sensu* Millidge (1995)
a.s.l.	above sea level
NHML	Natural History Museum, London, UK
C	convector *sensu* Tanasevitch (1998) = lamella *sensu* Merrett (1963)
D	duct
DAC	distal apophysis of convector *sensu* Tanasevitch (2015)
DSA	distal suprategular apophysis *sensu* Hormiga (2000)
E	embolus
MBC	main body of convector
N.P.	national park
PC	paraconvector *sensu* Tanasevitch (2014)

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Pr	protegulum
Re	receptacle
SD	seminal duct
T	tegulum
TmI	position of trichobothrium on metatarsus I

TAXONOMY

Genus *Nasoona* Locket, 1982

Type species: *Nasoona prominula* Locket, 1982 by original designation.

Taxonomic remarks: The genus includes medium-sized erigonines with a variegated abdomen and, in most cases, with a postocular elevation on the male carapace bearing a group of curved, spines, stout spines or setae.

Three species lack this carapace elevation: *N. asocialis* (Wunderlich, 1974), *N. chrysanthusi* Locket, 1982 and a new species described below.

The chaetotaxy formula is 2.2.1.1. Two exceptions given in the literature, 1.1.1.1 in *N. coronata* (Simon, 1894) and 1.1.1.1 in the male of *N. locketi* Millidge, 1995, are mistakes based on incomplete spination caused by partial loss of spines. Each metatarsus is with a trichobothrium, except for *N. coronata*.

The male palp is characterized by the following features:

1) highly modified palpal tibia;
2) poorly expressed distal suprategular apophysis;
3) reduction of median membrane and radix;
4) presence of convector (see Tanasevitch 1998, 2014);
5) presence of an additional sclerite in embolic division, named paraconvector (see Tanasevitch, 2014). At present the paraconvector is only known in *Nasoona*, but most probably this sclerite is more widely present among the Erigoninae. The embolus division of many taxa in this group is still poorly investigated.

The epigyne in *Nasoona* is typical for many erigonines and represented mostly by a shallow epigynal cavity which is sometimes divided by a septum and in a few species partially covered from above by an overhanging, visor-like outgrowth of the anterior epigynal wall. Receptacles are relatively small, subspherical or beanlike.

The position of the genus within the Erigoninae is unclear, but some somatic characters, i.e. chaeto- and trichobothriotaxy, modified male carapace, as well as genitalia conformation show similarity with *Gongylidioides* Oi, 1960 and in part *Oedothorax*.

Species included: Excluding one species which is removed from *Nasoona*, the genus currently comprises 17 species, 6 of them are described as new below.

Distribution: Extreme south of the Palaearctic Region: Nepal Himalayas and southern China; throughout the Oriental Region; Neotropical Region: Venezuela.

Range: Disjunct Oriental-Neotropical.

Nasoona indiana sp. nov.

Figs 1-3, 28-33

Holotype: Male; INDIA, West-Bengal, Darjeeling District, Ghoom, Tigerhill, southern slope, 2200-2300 m a.s.l., sifting in forest; 13.X.1978; leg. C. Besuchet & I. Löbl [#13].

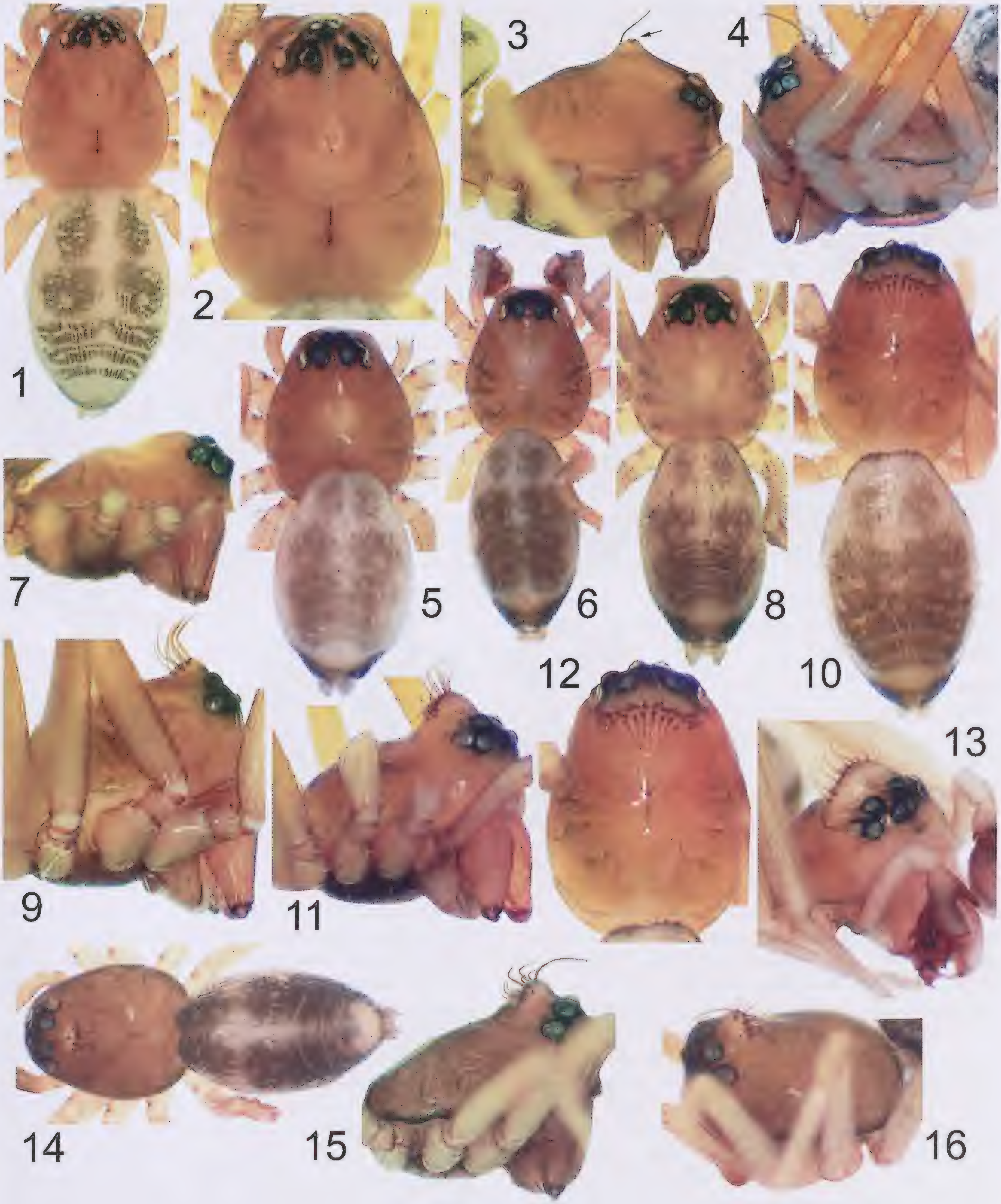
Diagnosis: According to the male palpal conformation, *N. indiana* sp. nov. seems to be most similar to *N. setifera* (Tanasevitch, 1998), known from a single locality in the mountains of Nepal (Tanasevitch, 1998). The new species differs by the bifid distal apophysis of the convector, by the slender distal process of the paraconvector which was erroneously named the suprategular apophysis (Tanasevitch, 1998), as well as by the shape of the carapace. The carapace of *N. indiana* sp. nov. has a small, conical postocular elevation bearing a stout seta, while in *N. setifera* the carapace is armed with several stout, bent spines and a seta situated on a huge postocular elevation. The shape of the carapace and the structure of the embolic division of *N. indiana* sp. nov. is also similar to that of *N. conica* (Tanasevitch, 1998), known from high altitudes of the Nepalense Himalayas, but the new species differs clearly by the shape of its palpal tibia.

Etymology: The specific epithet, a Latinized adjective, is derived from the name of the country of origin, India.

Description: *Male (holotype):* Total length 2.01. Carapace 1.13 long, 0.90 wide, pale reddish brown, with grey radial stripes and a narrow margin. Behind posterior median eyes a conical elevation with a socket terminally, indicated with arrow in Fig. 3, probably for a large, stout seta which was lost in this specimen (Figs 1-3). Chelicerae 0.55 long, unmodified. Legs yellow. Leg I 4.38 long (1.25+0.30+1.13+10.05+0.65), IV 4.44 long (1.25+0.28+1.13+1.15+0.63). Chaetotaxy: spines mostly lost, but probably 2.2.1.1. Each metatarsus with a trichobothrium. TmI 0.71. Palp (Figs 28-33): Tibia slightly expanded distally, with several very short spinules terminally. Retrolateral side of tibia with a tooth-like tubercle, prolateral side with a small dark protuberance and two larger keel-shaped outgrowths. Proximal part of paracymbium narrow, distal part expanded and bearing several weak spines. Tegulum terminating in transparent protegulum. Distal suprategular apophysis short, wide, T-shaped distally, bearing a black, sharp tooth in middle. Embolus long and thin, forming a loop, radix reduced. Main body of convector relatively narrow, twisted, its distal apophysis well-sclerotized, black, bifid. Paraconvector large, complicated, with a long, sabre-shaped distal process. Abdomen 1.40 long, 0.88 wide, dorsal pattern as in Fig. 1.

Female: Unknown.

Distribution: Only known from the type locality in the mountains of West-Bengal, India.



Figs 1-16. Photographs of *Nasoona indiana* sp. nov., male holotype (1-3); *N. orissa* sp. nov., male paratype (4); *N. intuberosa* sp. nov., male paratypes (5-7) and female paratype (8); *N. kinabalu* sp. nov., male holotype (9); *N. sabah* sp. nov., male paratype from Liwagu Trail (10-12) and male paratype from Silau-Silau Trail (13); *N. sulawesi* sp. nov., male holotype (14-16). (1, 5-6, 10, 14) Male body, dorsal view. (8) Female body, dorsal view. (2, 12) Male prosoma, dorsal view. (3-4, 7, 9, 11, 15) Male prosoma, lateral view. (13, 16) Male prosoma, anterolateral view. Not to scale.

Nasoona orissa sp. nov.

Figs 4, 34-41

Holotype: ZMMU; male; INDIA, Odisha State (= Orissa before 2011), road from Banigocha to Daspalla, near Padiakutibari, 20.382°N 84.771°E; 17.-25.I.2014; leg. K. Tomkovich.

Paratypes: ZMMU; 3 males; MHNG; 2 males; collected together with the holotype.

Diagnosis: The new species is characterized by the peculiar shape of the male papal tibia, by the distal apophysis of the convector which is divided into two lobes, as well as by a wide, strongly bent distal process of the paraconvector. The massive distal apophysis of the convector, as well as the shape of the distal process of the paraconvector of *N. orissa* sp. nov. resemble those of *N. crucifera*, which is widespread in the Oriental Region, but both species are clearly distinguished by the structure of the palpal tibia. The shape of the convector, as well as the strongly divided palpal tibia are similar to those of *N. sulawesi* sp. nov., but *N. orissa* sp. nov. can be easily distinguished by the shape of the distal process of the paraconvector.

Etymology: The specific epithet is a name in apposition referring to the "terra typica", the old name of the Odisha State in India.

Description:
Male (paratype): Total length 1.70. Carapace 0.75 long, 0.60 wide, pale brown, with a postocular elevation bearing bent, forward-directed, stout spines as shown in Fig. 4; eyes normal. Chelicerae 0.33 long, unmodified. Legs yellow. Leg I 2.61 long (0.70+0.18+0.68+0.63+0.42), IV 2.69 long (0.75+0.18+0.70+0.68+0.38). Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.52. Palp (Figs 34-41): Tibia divided into four lobes: prolateral one keel-shaped; dorso-prolateral one long, narrowing at middle; dorso-retrolateral one conical, with several very short spinules terminally; retrolateral outgrowth wide, forming a shallow cup. Proximal part of paracymbium narrow, L-shaped; distal part wide, ending in a hook. Distal suprategular apophysis short, flat, with a sharp, black tooth in middle. Embolus long and thin, forming a loop, radix reduced. Main body of convector relatively narrow, curved; its distal apophysis black, well sclerotized, divided into two uneven lobes with serrate walls. Paraconvector massive, complicated, with serrate edges and distinctly protruded distal process. Abdomen 1.00 long, 0.60 wide, dorsally white, with three longitudinal pairs of large, grey spots.
Female: Unknown.

Distribution: Only known from the type locality in western India.

Nasoona intuberosa sp. nov.

Figs 5-8, 17, 42-48

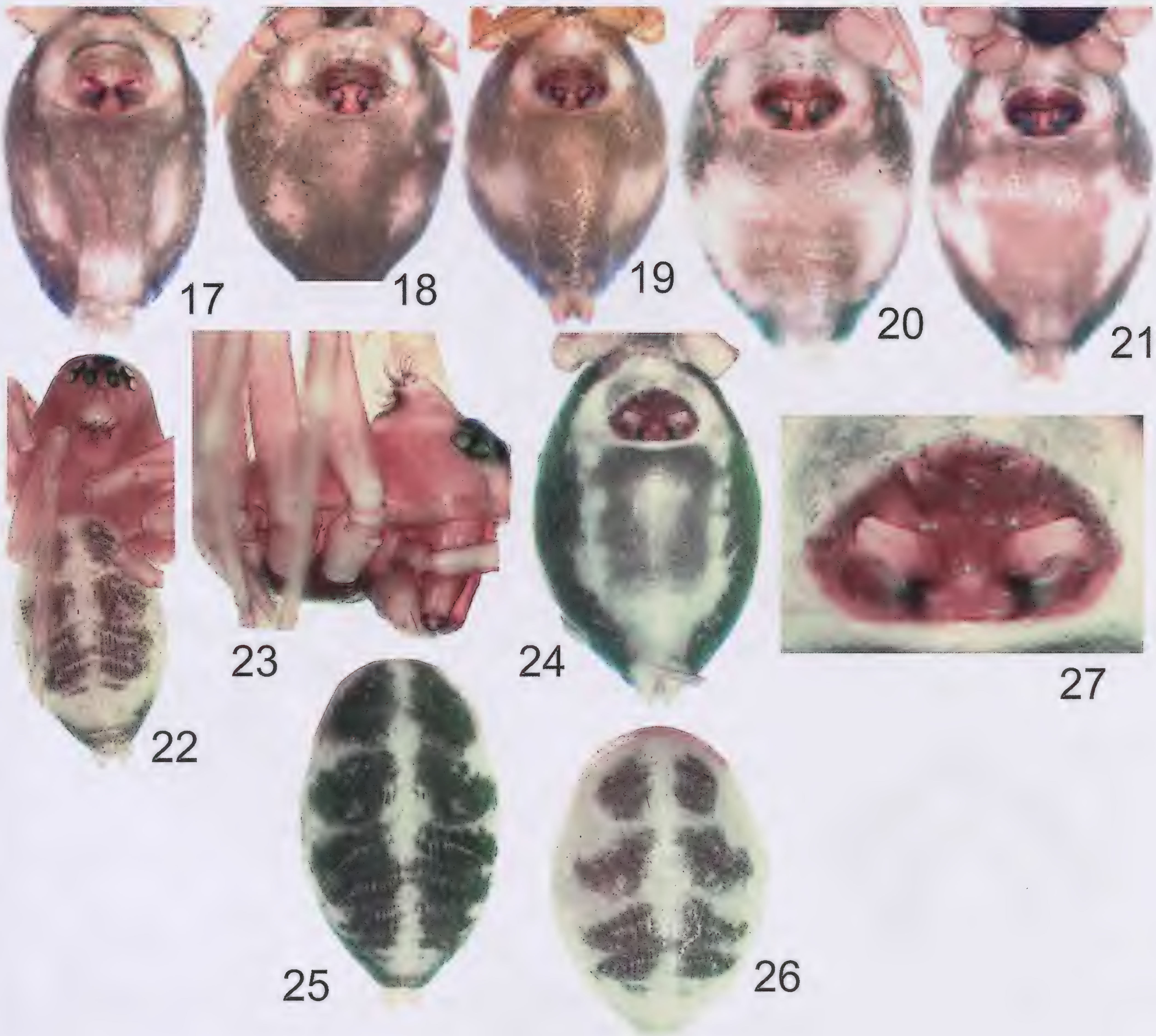
Holotype: Male; EAST MALAYSIA, Borneo, Sabah, Tambunan Distr., Crocker Range, 1550-1650 m a.s.l., near pass (road from Kota Kinabalu to Tambunan), *Lithocarpus* - *Castananopsis*, sifting decomposing wood, dead leaves and moss; 16.V.1987; leg. D. Burckhardt & I. Löbl [#27a].

Paratypes: 2 males, 3 females; collected together with the holotype.

Diagnosis: The new species is characterized by the unmodified carapace of males, which is untypical for the genus and previously known only from *N. asocialis* and *N. chrysanthusi*, as well as by the presence of two elongated pockets in the epigyne, similar to that of the Nepalense *N. comata*. Judging from the male palpal conformation, *N. intuberosa* sp. nov. is similar to two other new species described in here from the Mt Kinabalu, i.e., *N. kinabalu* sp. nov. and *N. sabah* sp. nov. From these two species *N. intuberosa* sp. nov. differs by the absence of a hump on the male carapace, by the shape of the palpal tibia, by details of the embolic division, as well as by the presence of two pockets divided by a relatively wide septum in the epigyne.

Etymology: The specific epithet is a Latin adjective referring to the absence of a hump on the male carapace, which is a characteristic feature for the genus *Nasoona*.

Description:
Male (paratype): Total length 1.65. Carapace 0.75 long, 0.65 wide, unmodified, pale brown, with grey radial stripes as shown in Figs 5-7; eyes normal. Chelicerae 0.35 long, unmodified. Legs yellow, pale brown. Leg I 3.21 long (0.83+0.23+0.82+0.78+0.55), IV 3.18 long (0.87+0.23+0.75+0.80+0.53). Chaetotaxy: spines mostly lost, but probably 2.2.1.1. Each metatarsus with a trichobothrium. TmI 0.61. Palp (Figs 42-46): Tibia relatively short, its retrolateral branch wide, with several very short spinules terminally, and with a black, pointed tubercle on its inner side. Prolateral branch well-sclerotized, stylet-shaped. Proximal part of paracymbium narrow, L-shaped; distal part wide, ending in a hook. Distal suprategular apophysis very short, flat, with a black, sharp tooth in middle, and with a transparent, narrow process terminally. Embolus long and thin, forming a loop, radix reduced. Main body of convector curved, its distal apophysis dark, narrow, serrate. Paraconvector large, with a long, claw-shaped distal process. Abdomen 0.95 long, 0.63 wide, dorsal pattern as shown in Figs 5-6.
Female (paratype): Total length 1.80. Carapace 0.80 long, 0.68 wide, unmodified, pale brown, with grey, radial stripes, as shown in Fig. 8. Chelicerae 0.35 long, unmodified. Legs pale brown. Leg I 3.21 long (0.88+0.25+0.78+0.75+0.55), IV 3.16 long (0.88+0.25+0.78+0.80+0.45). Legs yellow, pale brown.



Figs 17-27. Photographs of *Nasoona intuberosa* sp. nov., female paratype (17); *N. kinabalu* sp. nov., female paratype from Mt Kinabalu, 3150-3200 m (18) and female paratype from Mt Kinabalu, 2590 m (19); *N. sabah* sp. nov., female paratype from Silau-Silau Trail (20) and female paratype from Liwagu Trail (21); *N. comata* (Tanasevitch, 1998), specimens from Hellok, Nepal (22-27).
(17-21, 24) Female abdomen, ventral view. (22) Male body, dorsal view. (23) Male prosoma, lateral view. (25-26) Female abdomen, dorsal view. (27) Epigyne, ventral view. Not to scale.

Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.62. Abdomen 1.03 long, 0.65 wide, as shown in Fig. 8. Epigyne (Figs 17, 47-48) with two shallow elongated pockets; seminal ducts wide, S-shaped; receptacles subspherical.

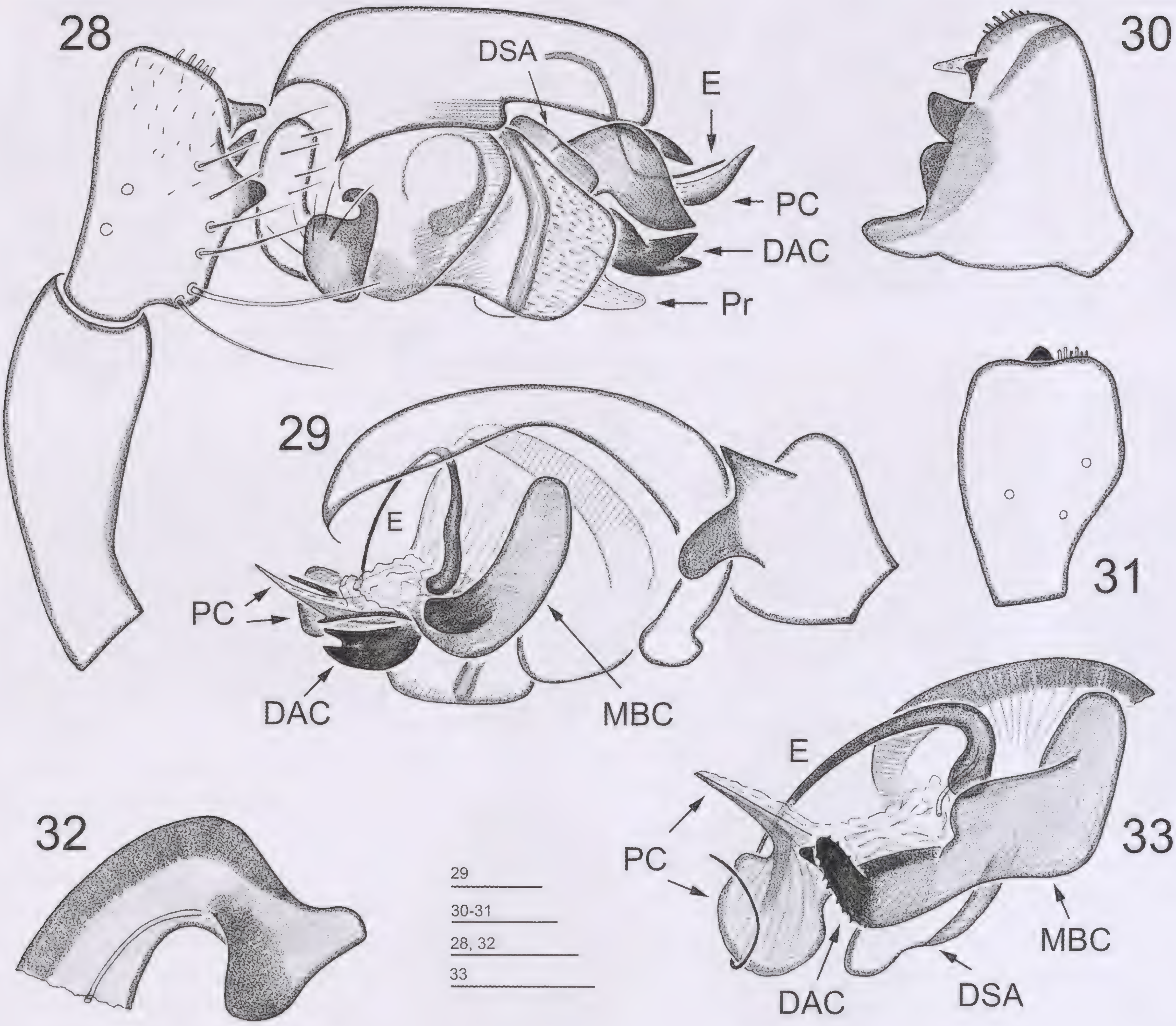
Distribution: Only known from the type locality in the Crocker Range on Borneo, East Malaysia.

Nasoona kinabalu sp. nov.

Figs 9, 18-19, 49-55

Holotype: Male; EAST MALAYSIA, Borneo, Sabah, Kinabalu N.P., Mt Kinabalu, below Layang-Layang, 2600 m a.s.l., interception trap; 2.-8.V.1987; leg. A. Smetana [#B20].

Paratypes: 1 male; Mt Kinabalu, below Layang-Layang, 2595 m a.s.l.; 2.V.1987; leg. A. Smetana [#B19]. – 1 male, 3 females; Mt Kinabalu, 2590 m a.s.l., humid ravine below Layan Layang, cloud forest, sifting



Figs 28-33. *Nasoona indiana* sp. nov., holotype. (28-29) Right palp, retrolateral and prolateral view, respectively. (30-31) Palpal tibia, prolateral and dorsal view, respectively. (32) Distal suprategular apophysis. (33) Distal suprategular apophysis and embolic division.

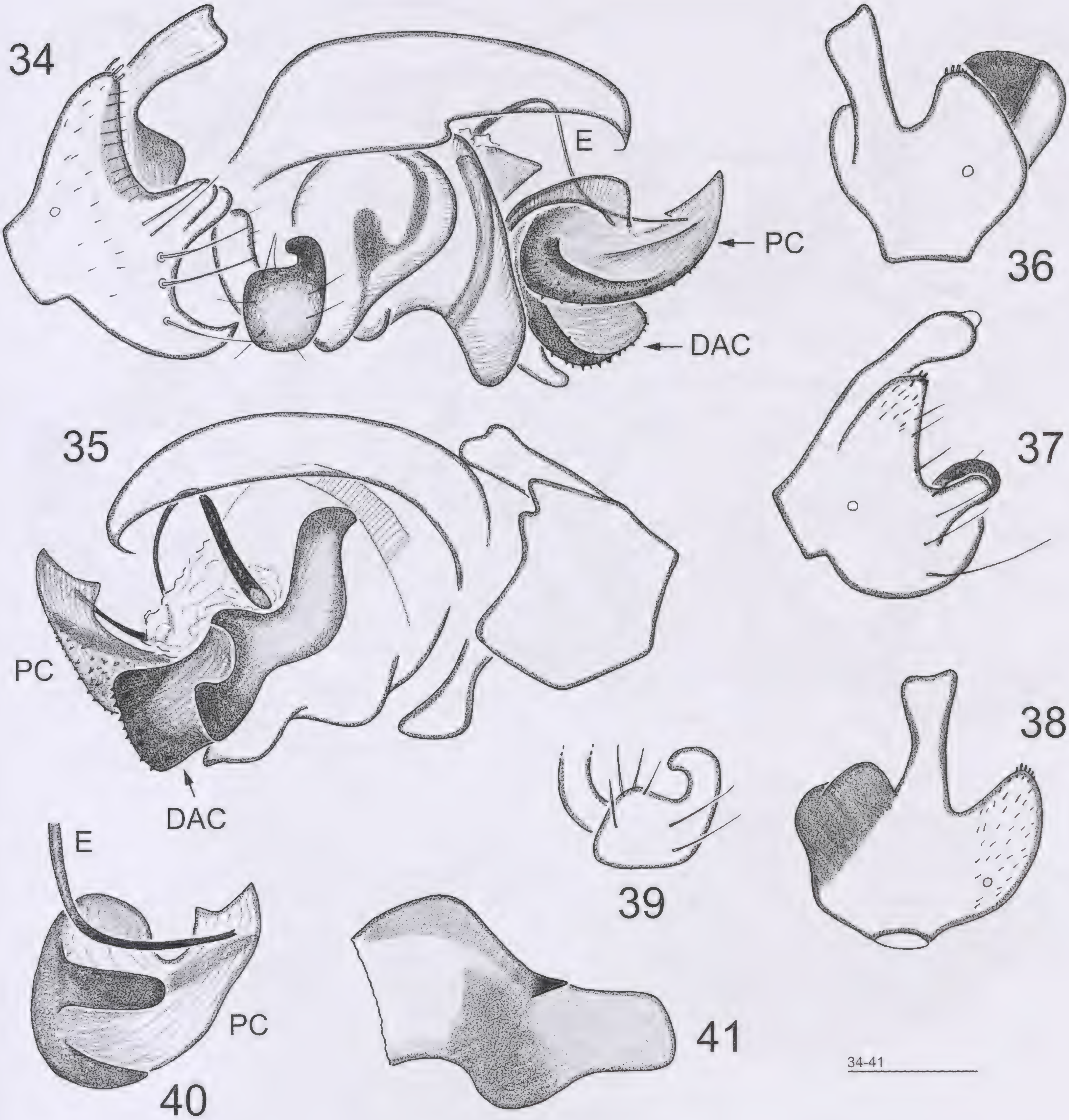
leaf litter in humid ravine; 1.V.1987; leg. D. Burckhardt & I. Löbl [#10a]. – 1 male, 1 female; Mt Kinabalu, 3150-3200 m a.s.l., humid Myrtaceae and Ericaceae forest, sifting moss and fern near Paka cave, near river; 3.V.1987; leg. D. Burckhardt & I. Löbl [#12b].

Diagnosis: The species appears to be most similar to *N. sabah* sp. nov., and differs by the shorter retrolateral outgrowth of the male palpal tibia, by the shape of the paraconvector, as well as by the presence of a bipartite visor-like structure above the epigynal cavity.

Etymology: The specific epithet is a name in apposition referring to the "terra typica", Mt Kinabalu on Borneo.

Description:

Male (paratype from Mt Kinabalu, 2590 m a.s.l.): Total length 1.90. Carapace 0.95 long, 0.75 wide, pale brown, with grey radial stripes and a narrow margin. Postocular elevation bearing bent, forward-directed stout spines as shown in Fig. 9; eyes normal. Chelicerae 0.95 long, unmodified. Legs pale brown. Leg I 3.63 long (1.00+0.25+0.95+0.83+0.60), IV 3.66 long (1.03+0.25+0.93+0.85+0.60). Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.70. Palp (Figs 49-53): Tibia relatively short, its retrolateral branch wide, with several very short spinules terminally and with a black, rounded tubercle on its inner side. Prolateral branch well-sclerotized, dagger-shaped. Paracymbium widened distally, ending in a hook. Distal suprategular apophysis short, flat, with a shallow distally and with a black, sharp tooth in middle. Embolus long and thin, forming a loop, radix reduced. Main body of convector narrow, curved; its distal apophysis black, well sclerotized, serrate, rounded apically. Paraconvector massive, complicated, serrate; distal process distinctly



Figs 34-41. *Nasoona orissa* sp. nov., male paratype. (34-35) Right palp, retrolateral and prolateral view, respectively. (36-38) Palpal tibia, retrodorsal, retrolateral and dorsal view, respectively. (39) Paracymbium. (40) Distal suprategular apophysis. (41) Distal part of embolus and paraconvector.

protruded. Abdomen 1.00 long, 0.60 wide, dorsally white, with three longitudinal pairs of large, grey spots.

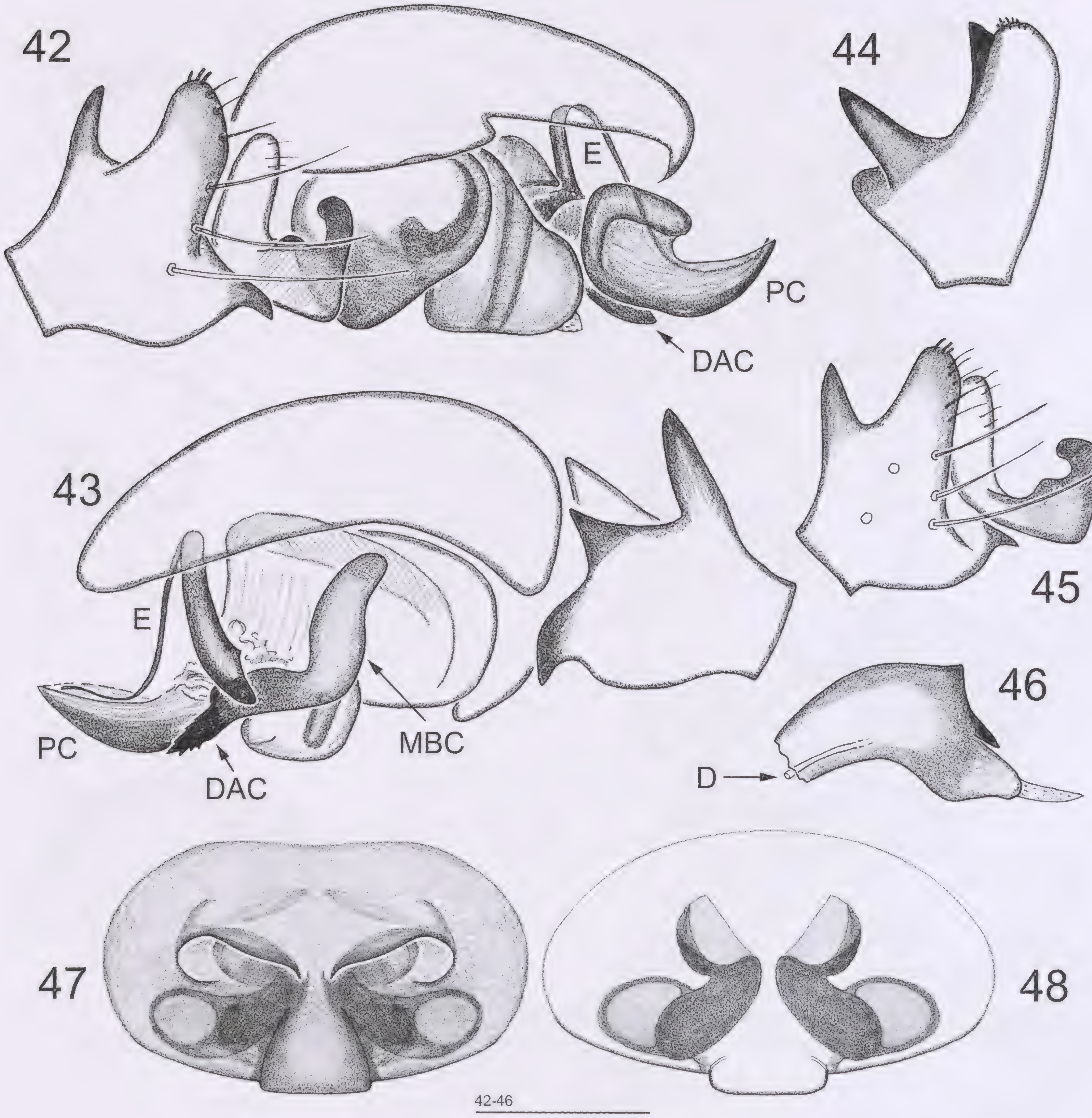
Female (paratype from Mt Kinabalu, 2590 m a.s.l.): Total length 2.52. Carapace 1.00 long, 0.85 wide, pale greyish brown, with grey radial stripes and a narrow margin; unmodified. Chelicerae 0.45 long, unmodified. Legs pale brown. Leg I 3.90 long (1.05+0.30+1.03+0.90+0.62), IV 4.11 long (1.15+0.30+1.03+1.05+0.58). Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.71. Epigyne (Figs 18-19, 54-55): Anterior wall with a bipartite visor-like outgrowth overhanging epigynal cavity. Seminal ducts wide, shaped like a question mark, receptacles beanlike. Abdomen 1.50 long, 1.15 wide, dorsally with two rows of almost merged grey spots.

Distribution: Only known from highlands of Mt Kinabalu on Borneo, East Malaysia.

Nasoona sabah sp. nov.

Figs 10-13, 20-21, 56-63

Holotype: Male; EAST MALAYSIA, Borneo, Sabah, Kinabalu N.P., Mt Kinabalu, 1550-1650 m a.s.l., Silau-



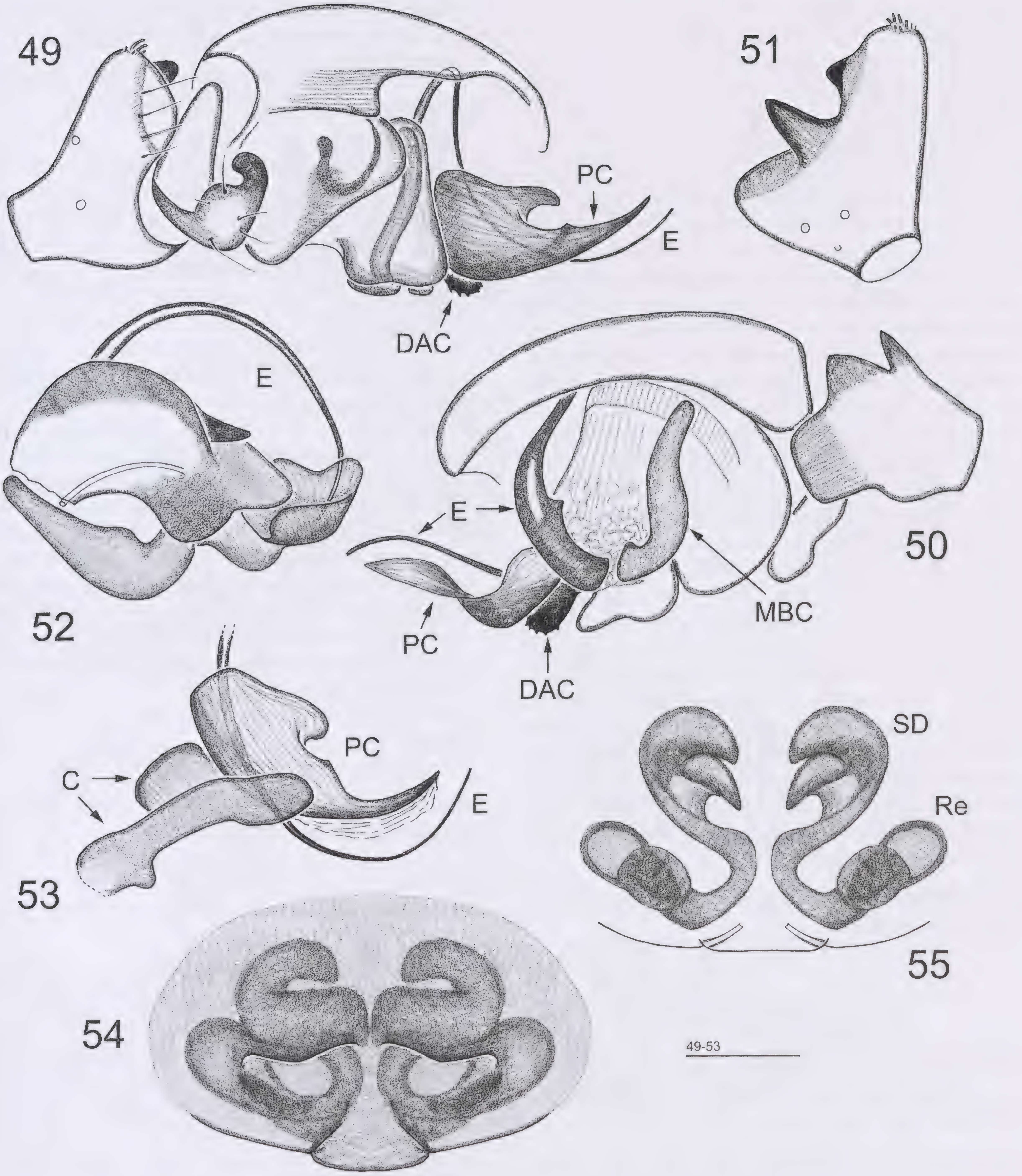
Figs 42-48. *Nasoona intuberosa* sp. nov., male and female paratypes. (42-43) Right palp, retrolateral and prolateral view, respectively. (44) Palpal tibia, dorsal view. (45) Palpal tibia and paracymbium, retrodorsal and very slightly proximal view. (46) Distal suprategular apophysis. (47) Epigyne, ventral view. (48) Cleared epigyne, dorsal view.

Silau Trail, *Lithocarpus-Castanopsis* forest, sifting decomposing wood and dead leaves in humid ravine; 24.IV.1987; leg. D. Burckhardt & I. Löbl [#2a].

Paratypes: 2 males, 5 females; collected together with the holotype. – 1 male, 2 female; Mt Kinabalu, 1540 m a.s.l., Liwagu Trail, sifting leaf litter in small ravine and at base of old trees; 29.IV.1987; leg. D. Burckhardt & I. Löbl [#8a]. – 1 female; Mt Kinabalu, 1750 m a.s.l., Liwagu Trail, sifting bark, decomposing wood and leaf litter next to a log and at base of tree stumps; 27.IV.1987; leg. D. Burckhardt & I. Löbl [#5a]. – 6 females; Mt Kinabalu, 1500 m a.s.l., Liwagu Trail, section 2, *Lithocarpus* & *Podocarpus* forest, Silau-Silau Trail, *Lithocarpus-Podocarpus* forest, sifting moss and dead leaves along Silau-Silau Trail; 21.V.1987; leg. D. Burckhardt & I. Löbl [#34b].

Other material examined: Male holotype of *Pronasoona sylvatica* Millidge, 1995; Kinabalu N.P., Poring Hot Springs.

Diagnosis: The new species is characterized by the shape of the postocular elevation on the male carapace which looks like a transverse ridge similar to that in *Pronasoona sylvatica*, but *P. sylvatica*, has only one row of spines on the elevation, *N. sabah* sp. nov. has



Figs 49-55. *Nasoona kinabalu* sp. nov., male and female paratypes from Mt Kinabalu, 2590 m. (49-50) Right palp, retrolateral and prolateral view, respectively. (51) Palpal tibia, dorsal view. (52) Distal suprategular apophysis and embolic division. (53) Convector, paraconvector and distal part of embolus. (54) Epigyne, ventral view. (55) Cleared epigyne, dorsal view.

two rows of bent, stout spines. According to the male palp structure the new species appears most similar to *N. kinabalu* sp. nov. (see above). The epigyne of *N. sabah* sp. nov. resembles that of *N. chrysanthusi*, but differs by the shape of the translucent seminal ducts.

Etymology: The specific epithet is a name in apposition referring to the "terra typica", the Sabah State of East Malaysia on Borneo Island.

Description:

Male (paratype from Silau-Silau Trail): Total length 2.02. Carapace 0.93 long, 0.70 wide, pale brown, with grey radial stripes and a narrow margin. A transverse

postocular ridge slightly bent forward and bearing two rows of curved, stout spines. Spines of anterior row directed forward, those of posterior row directed backwards, as shown in Figs 10-13; eyes normal. Chelicerae 0.35 long, unmodified. Legs pale brown. Leg I 3.26 long (0.88+0.20+0.85+0.80+0.53), IV 3.23 long (0.90+0.22+0.83+0.80+0.48). Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.60. Palp (Figs 56-61): Retrolateral branch of palpal tibia relatively long and wide, with several very short spinules terminally and with a black rounded tubercle on its inner side. Prolateral branch strongly sclerotized, dagger-shaped. Paracymbium L-shaped, ending with a hook. Distal suprategular apophysis short, flat, narrow, with a black, sharp tooth in middle. Embolus long and thin, forming a loop, radix reduced. Main body of convector curved, its distal apophysis dark, narrow, serrate. Paraconvector large, complicated, with a long, claw-shaped distal process. Abdomen 1.28 long, 0.70 wide, dorsal pattern as shown in Fig. 10.
Female (paratype from Silau-Silau Trail): Total length 2.15. Carapace 0.95 long, 0.70 wide, unmodified. Chelicerae 0.43 long, unmodified. Legs pale brown. Leg I 3.41 long (0.95+0.25+0.88+0.83+0.50), IV 3.46 long (1.00+0.25+0.90+0.83+0.48). Chaetotaxy: 2.2.1.1, length of spines about 1.5-3 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.60. Abdomen 1.38 long, 0.85 wide, dorsally white and with indistinct grey pattern. Epigyne (Figs 20-21, 62-63): anterior wall forming an angle slightly overhanging wide, shallow epigynal cavity. Seminal ducts very wide, receptacles subspherical.

Distribution: Only known from Mt Kinabalu on Borneo, East Malaysia.

Nasoona sulawesi sp. nov.
Figs 14-16, 64-69

Holotype: Male; INDONESIA, northern Sulawesi, Kotamobagu, Matali Baru, road to Torosik, Mt Tongara, 600-900 m a.s.l.; 5.XII.1999; leg. A. Riedel.

Other material examined: Male holotype and 2 females paratypes of *Nasoona silvestris* Millidge, 1995 from Sumba Island, Indonesia.

Diagnosis: The new species appears most similar to the Neotropical *N. coronata*, known from San Esteban N.P., Venezuela. This similarity is seen the palpal structure, namely in the shape of the large, strongly sclerotized convector and paraconvector. *Nasoona sulawesi* sp. nov. is also somewhat similar to *N. crucifera*, which is widespread in the Oriental Region (World Spider Catalog, 2017) and to *N. silvestris*, described from Sumba, Indonesia (Millidge, 1995). *Nasoona sulawesi* sp. nov. is distinguished from the above-mentioned species by the shape of the strongly modified palpal tibia and by details of the palpal sclerites.

Etymology: The specific epithet is a name in apposition referring to the "terra typica", Sulawesi Island.

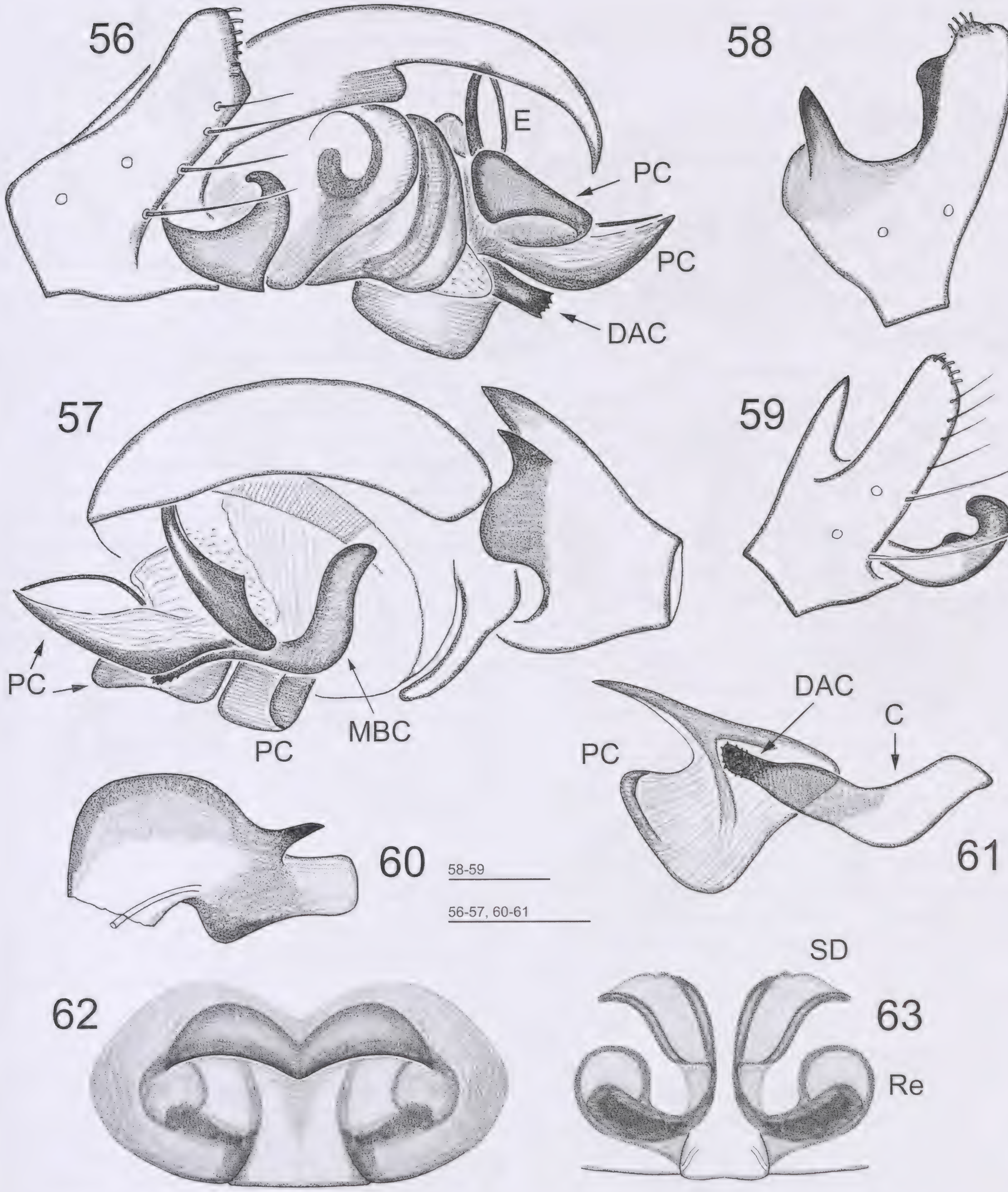
Description:
Male (holotype): Total length 1.83. Carapace 0.85 long, 0.70 wide, greyish brown, with a postocular elevation bearing bent, stout spines as shown in Figs 14-16; occipital region of elevation with a small hollow bearing very short hairs as shown in Fig. 15; eyes normal. Chelicerae 0.30 long, unmodified. Legs yellow. Leg I 3.06 long (0.85+0.23+0.83+0.75+0.50), IV 3.14 long (0.85+0.23+0.80+0.78+0.48). Chaetotaxy: 2.2.1.1, length of spines about 1.5-2.5 diameters of leg segment. Each metatarsus with a trichobothrium. TmI 0.53. Palp (Figs 64-69): Tibia divided into four parts of different shapes. Dorsal branch of palpal tibia with several very short spinules terminally. Proximal part of paracymbium narrow, L-shaped; distal part wide, bearing several weak spines, ending with a hook. Distal suprategular apophysis short, flat, rounded distally, with a sharp black tooth in middle. Embolus long and thing, forming a loop; radix reduced. Main body of convector massive, black, distally divided by a narrow cleft into two parts, these serrate distally. Paraconvector large, complicated, with a long, claw-shaped distal process. Abdomen 1.01 long, 0.65 wide, dorsally dark grey, with a white, median stripe as shown in Fig. 14.
Female. Unknown.

Distribution: Only known from the type locality in northern Sulawesi, Indonesia.

Nasoona comata (Tanasevitch, 1998)
Figs 22-27

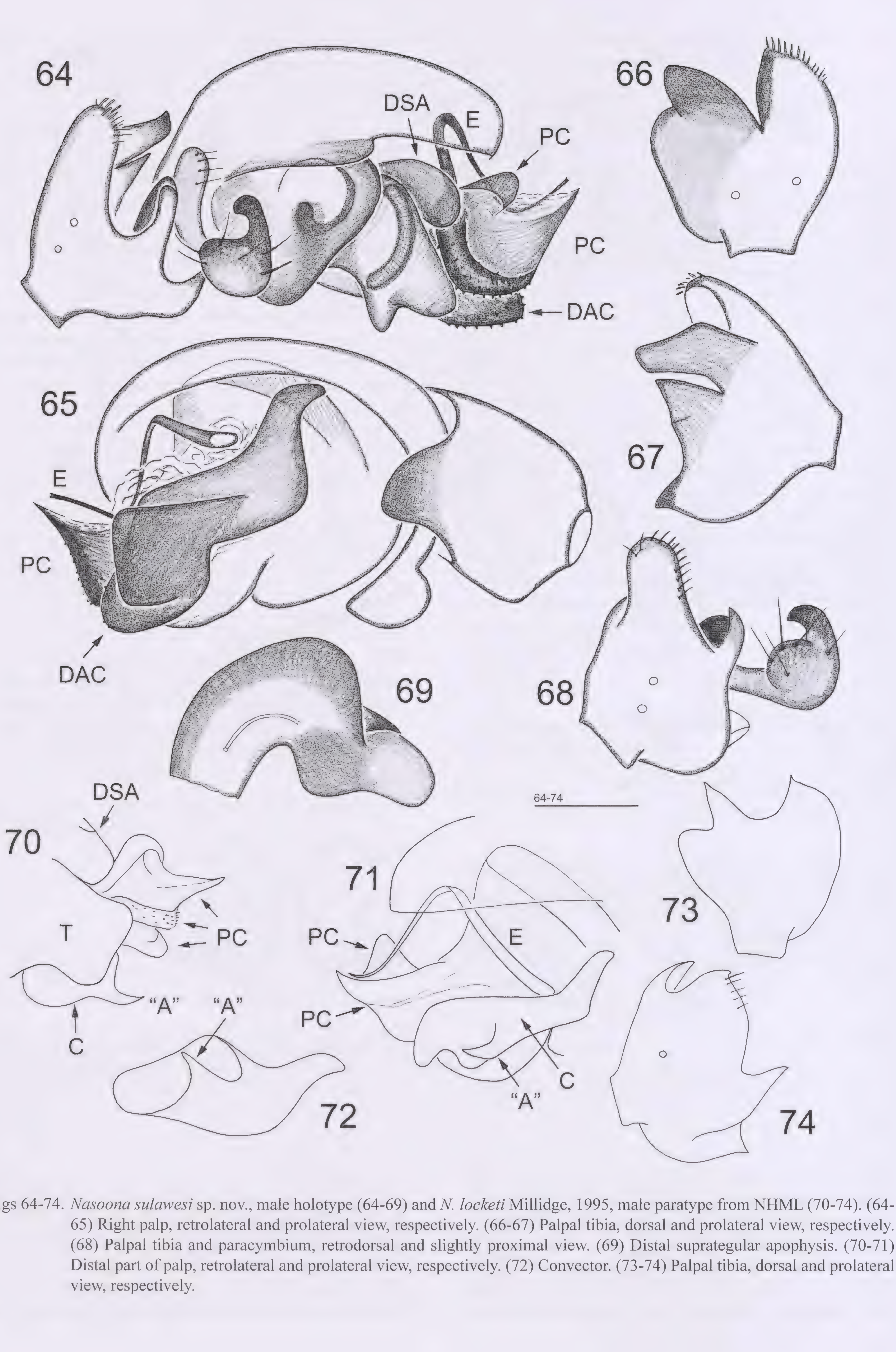
Remarks: This Nepalense species was hitherto known from males only (Tanasevitch, 1998). When re-examining material collected during Jochen Martens' expeditions to Nepal and kept at the SMF, the unknown females were found. The male of *N. comata* was described in detail earlier (see Tanasevitch, 1988), therefore I here only give photos of the male body (Fig. 22) and prosoma (Fig. 23). The first description of the female of *N. comata* is given below.

Material examined: All specimens in SMF: 1 male, 6 females; NEPAL, Taplejung Distr., Hellok in Tamur Valley, 2000 m a.s.l., forest remnant, bushes; 17.V.1988; leg. J. Martens & W. Schawaller [#371]. – 5 females; Ilam Distr., Mai Pokhari, 2100-2200 m a.s.l., forest; 25.-27.III.1980; leg. J. Martens & A. Ausobsky [#116]. – 1 female; same locality, 2100 m a.s.l., forest; 31.III.-1.IV.1980; leg. J. Martens & A. Ausobsky [#117]. – 4 females; Taplejung Distr., Grat Lasse Dhara and Aim Lassetham, 3000-3300 m a.s.l.; 6.-7.IX.1983; leg. J. Martens & B. Daams [#275]. – 1 female; SE



Figs 56-63. *Nasoona sabah* sp. nov., male and female paratypes from Mt Kinabalu, 1540 m. (56-57) Right palp, retrolateral and prolateral view, respectively. (58) Palpal tibia, dorsal view. (59) Palpal tibia and paracymbium, retrodorsal and slightly proximal view. (60) Distal suprategular apophysis. (61) Paraconvector and convector. (62) Epigyne, ventral view. (63) Cleared epigyne, dorsal view.

Yamputhin, l650-2000 m a.s.l., forest mainly *Alnus*; 26. & 30.IV.1988; leg. J. Martens & W. Schawaller [#350]. – 3 females; Yamputhin cultural land, 1650-1800 m a.s.l., open forest; 26.IV-1.V.1988; leg. J. Martens & W. Schawaller [#351]. – 5 females; Omje Kharka NW Yamputhin, natural mixed broadleaved forest, 2300-2500 m a.s.l.; 1.-6.V.1988; leg. J. Martens & W. Schawaller [#356]. – 2 females; pasture Lassetham NW of Yamputhin, 3300-3500 m a.s.l., mature *Abies-Rhododendron* forest; 6.-9.V.1988; leg. J. Martens & W. Schawaller [# 59]. – 1 female; upper Simbua Khola, ascent to pasture Lassetham, 3000-3150 m a.s.l.,



Figs 64-74. *Nasoona sulawesi* sp. nov., male holotype (64-69) and *N. locketi* Millidge, 1995, male paratype from NHML (70-74). (64-65) Right palp, retrolateral and prolateral view, respectively. (66-67) Palpal tibia, dorsal and prolateral view, respectively. (68) Palpal tibia and paracymbium, retrodorsal and slightly proximal view. (69) Distal suprategular apophysis. (70-71) Distal part of palp, retrolateral and prolateral view, respectively. (72) Convector. (73-74) Palpal tibia, dorsal and prolateral view, respectively.

mature mixed *Tsuga-Rhododendron* broadleaved forest; 15.V.1988; leg. J. Martens & W. Schawaller [#364]. – 1 male, 6 females; Hellok in Tamur Valley, 2000 m a.s.l., forest remnant, bushes; 17.V.1988; leg. J. Martens & W. Schawaller [#371]. – 3 females; Panchthar Distr., Paniporua, 2300 m a.s.l., mixed broadleaved forest; 16.-20.IV.1988; leg. J. Martens & W. Schawaller [#328]. – 1 female; between Paniporua and Hinwa Khola Valley, 1850-2300 m a.s.l., cultivated land, tree-rich; 20.IV.1988; leg. J. Martens & W. Schawaller [#329].

Description:
Female (specimen from Hellok): Total length 2.30. Carapace 1.15 long, 0.80 wide, unmodified, reddish brown, with a narrow, grey margin. Chelicerae 0.45 long. Legs pale brown. Leg I 4.33 long (1.25+0.30+1.13+1.00+0.65), IV 4.30 long (1.20+0.30+1.10+1.10+0.60). Chaetotaxy 2.2.1.1. Each metatarsus with a trichobothrium. Tm I 0.68. Abdomen 1.25 long, 0.85 wide, dorsal pattern as shown in Figs 25-26. Epigyne (Figs 24, 27) with elongated pockets divided with relatively wide septum. Seminal ducts wide, receptacles oval.

Taxonomic remarks: According to genitalia conformation, *N. comata* appears most similar to the Bornean *N. intuberosa* sp. nov. The male of *N. comata* can be easily distinguished from that of *N. intuberosa* sp. nov. by the presence of a hump on the male carapace bearing a group of bent, stout spines (see Figs 22-23), as well as by the shape of the palpal tibia. Females differ by more widely separated pockets of the epigyne in *N. comata*.

Distribution: The species has hitherto been known from 1650-2300 m a.s.l. in the Ilam, Panchithar and Taplejung districts in Nepal. The new records expand the known distribution of this species in Nepal, and its altitudinal range to 3500 m a.s.l.

Nasoona locketi Millidge, 1995
Figs 70-74

Type material examined: NHML #bm.1995-7-25-12; female holotype of *Nasoona locketi*; Rakata, Krakatoa, Sept. 1984 (Latrobe Exped.). – NHML #bm.1995-7-25-11; male paratype of *Nasoona locketi*; Rakata, Krakatoa, Sept. 1984. (Latrobe Exped.).

Remarks: The species was originally described from both sexes from Krakatoa Island, Indonesia (Millidge, 1995). As mentioned above, the untypical chaetotaxy in the male (1.1.1.1 instead of 2.2.1.1) is the result of an incorrect count of the number of spines caused by partial loss. The figures of the male palp given by the author for *N. locketi* (see Millidge, 1995: figs 27-29) do not accurately reflect its structure, therefore I give new schematic drawings of the male paratype here (see Figs 70-74). The "basal apophysis of the embolic division" of Millidge (1995: 45), which is marked in figs 24 and 28 as "A" [the same in fig. 23 for *N. coronata*], is indeed an apophysis of the convector.

Nasoona chrysanthusi Locket, 1982

New material examined: 1 female; INDONESIA, Sumatra, West Sumatra Province, Rimbo Panti N.R., ca 30 km N of Lubuksikaping, 0°20'46"N 100°04'09"E, 300-400 m a.s.l., primary forest; 11. & 13.VI.2006; leg. P. Schwendinger [Sum-06/18]. – 1 female; Panti, 250 m a.s.l., sifting of vegetational debris in lowland swamp forest; 19.XI.1989; leg. D. Burckhardt, I. Löbl and D. Agosti [#23].

Distribution: The species was previously known from Malaysia and Singapore (World Spider Catalog, 2017) and is here also reported from Indonesia.

Nasoona crucifera (Thorell, 1895)

New material examined: SMF; 1 male, 1 female; TAIWAN, Pingtung County, Kenting, close to Howard Beach Resort, 21°56'17.63"N 120°48'31.85"E, 24 m a.s.l., secondary forest, at night, by hand; 24.VI.2013; leg. P. Jäger. – 1 female; Pingtung County, Hengchun Township, near Kenting Youth Activities Center, decaying wood and adjacent litter; 3.I.2012; leg. S. Vit [TAIW-11-12/5]. – 1 male; HONG KONG, Victoria Peak, environs of Hong Kong University, 150 m a.s.l.; 30.XI.1988; leg. C. Lienhard [Bru-88/53].

Distribution: The species was previously known from India, Myanmar, Thailand, Laos, Vietnam, Singapore, Malaysia, Indonesia, China (World Spider Catalog, 2017) and is here also reported from Taiwan and Hong Kong.

Nasoona prominula Locket, 1982

New material examined: SMF; 1 male, 1 female; TAIWAN, Pingtung County, Kenting, close to Howard Beach Resort, 21°56'17.63"N 120°48'31.85"E, 24 m a.s.l., secondary forest, at night, by hand; 24.VI.2013; leg. P. Jäger.

Remarks: The species was previously known from Thailand, Laos, Malaysia, Singapore (World Spider Catalog, 2017) and is here also reported from Taiwan.

Oedothorax nigromaculatus (Gao, Fei & Xing, 1996) comb. nov.

Nasoona nigromaculata Gao, Fei & Xing, 1996: 29, figs 1-5.

Remarks Type material: The type material had been deposited at the Department of Cellular Biology,

Norman Bethune University of Medical Sciences (Changchun, China), but according to Shou-Wang Lin is now lost (pers. comm.).

Taxonomic remarks: This species was originally described from specimens collected in the Anhui and Zhejiang provinces of China and placed in the genus *Nasoona*. Despite the poorly drawn genitals, it is quite obvious that the species actually belongs to *Oedothorax*. The transfer proposed here is also supported by the same chaetotaxy (2.2.1.1), by the presence of a trichobothrium on metatarsus IV, as well as by the similar conformation of genitals.

CONCLUSION

Taking into account the new data, the genus *Nasoona* now comprises 16 nominal species mostly distributed in the Oriental Region. Two species, *N. indiana* sp. nov. and *N. orissa* sp. nov., are known from India. Three species, *N. asocialis*, *N. crucifera* and *N. prominula*, are widespread throughout the region, and the northern margin of their geographical ranges slightly extend into the Palaearctic, i.e. into Nepal and southern China. *Nasoona chrysanthusi* is still known only from the Malay Peninsula and Sumatra. Four species, *N. comata*, *N. conica*, *N. setifera* and *N. wunderlichi*, occur in the highlands of Nepal, just near the border of the Palaearctic and the Oriental regions. Six species are known only from Southeast Asian islands: *N. kinabalu* sp. nov., *N. intuberosa* sp. nov. and *N. sabah* sp. nov. from Borneo; *N. locketi* from Krakatoa, *N. silvestris* from Sumba, *N. sulawesi* sp. nov. from Sulawesi. One congener, *N. coronata* (type specimen in the National Museum of Natural History in Paris examined), is known from Venezuela in the Neotropics. This is rather unusual and could be based on a confusion of labels. Therefore a confirmation of this record by newly collected specimens from Venezuela is desirable. According to the current data, the geographical range of the genus can be characterized as disjunct Oriental-Neotropical.

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REFERENCES

Förster A., Bertkau P. 1883. Beiträge zur Kenntniss der Spinnenfauna der Rheinprovinz. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens* 40: 205-278.

Gao J.C., Fei R., Xing S.Y. 1996. A new species of the genus *Nasoona* from China (Araneae: Linyphiidae: Erigoninae). *Acta Zootaxonomica Sinica* 21: 29-31.

Hormiga G. 2000. Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). *Smithsonian Contributions to Zoology* 609: 1-160.

Locket G.H. 1982. Some linyphiid spiders from western Malaysia. *Bulletin of the British Arachnological Society* 5: 361-384.

Merrett P. 1963. The palpus of male spiders of the family Linyphiidae. *Proceedings of the Zoological Society of London* 140: 347-467.

Millidge A.F. 1995. Some linyphiid spiders from south-east Asia. *Bulletin of the British Arachnological Society* 10: 41-56.

Oi R. 1960. Linyphiid spiders of Japan. *Journal of the Institute of Polytechnics Osaka City University* 11(D): 137-244.

Simon E. 1894. Histoire naturelle des araignées, vol. 1. *Roret, Paris,* pp. 489-760.

Tanasevitch A.V. 1998. *Gorbothorax* n. gen., a new linyphiid spider genus from the Nepal Himalayas (Arachnida, Araneae, Linyphiidae). *Bonner Zoologische Beiträge* 47: 421-428.

Tanasevitch A.V. 2014. New species and records of linyphiid spiders from Laos (Araneae, Linyphiidae). *Zootaxa* 3841(1): 67-89.

Tanasevitch A.V. 2015. Notes on the spider genus *Oedothorax* Bertkau, 1883 with description of eleven new species from India (Linyphiidae: Erigoninae). *Revue suisse de Zoologie* 122(2): 381-398.

Thorell T. 1895. Descriptive catalogue of the spiders of Burma, based upon the collection made by Eugene W. Oates and preserved in the British Museum. *British Museum (Natural History), London*, 406 pp.

World Spider Catalog 2017. World Spider Catalog, version 18.5. Natural History Museum Bern. Online at http://wsc.nmbe.ch (accessed in October, 2017).

Wunderlich J. 1974. Linyphiidae aus Nepal, II. Die Gattung *Oedothorax* Bertkau 1883 (Arachnida: Araneae). *Senckenbergiana biologica* 55: 169-188.

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DNA barcoding of some Pandeidae species (Cnidaria, Hydrozoa, Anthoathecata)

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Abstract: Using 16S, COI, and ITS DNA sequences, it was possible to link a Norwegian marine hydroid formerly known as *Leuckartiara abyssi* (G.O. Sars, 1874) to a *Neoturris* medusa occurring in the same region. Although the Norwegian medusae showed some slight morphological differences to Mediterranean *Neoturris pileata*, DNA sequence comparisons show that they must be conspecific. A Mediterranean specimen of *N. pileata* showed less sequence divergences to the Norwegian *Neoturris* than was found within this latter population. The morphological differences are likely only age- and environmentally related. *Leuckartiara abyssi* is thus a subjective synonym of *Neoturris pileata* (Forsskål, 1775). The sequence analyses were embedded in a comparison with other members of the family Pandeidae. Contrary to the case for most other hydrozoans investigated, 16S sequences show very little divergences within the genus *Catablema* and it is thus not a good barcoding marker for this genus. COI sequences showed about three times greater divergence than 16S within selected pandeid species clades and are more suitable to investigate *Catablema* species, although also for COI the divergences within this group remain rather small. *Catablema nodulosum* Bigelow, 1913 was found to be most likely conspecific with *Catablema vesicarium* (A. Agassiz, 1862) and was therefore accepted only as a subspecies of the latter, thus following the opinion of most other prominent taxonomists of the last century. Medusae referred to *Catablema multicirratum* Kishinouye, 1910 originating from either the NE Pacific or the Eurasian sector of the Arctic Sea could belong to two distinct species.

The medusa *Leuckartiara longicalcar* n. spec. is described and illustrated. It occurs along the coast of North America from British Columbia to California and has been confused previously with *L. octona* (Fleming, 1823).

Keywords: *Neoturris pileata* - life cycle - barcoding - systematics - *Catablema* - *Leuckartiara* - new species - hydromedusae.

INTRODUCTION

The family Pandeidae is a group of anthoathecate hydrozoans with a cosmopolitan distribution, currently comprising 89 accepted species (Schuchert, 2017a). The family is somewhat unique among the Order Anthoathecata as many species have relatively large and conspicuous medusae (Figs 5-7, 10-16). They can occasionally be found caught in large numbers in rock-pools or protected bays and thus attract the interest of non-specialist naturalists. In contrast to the medusae, their hydroid stages are often small, rather uniform in morphology, and difficult to identify to species level. For the majority of the Pandeidae species, only the medusa phase of the life cycle is known, while their hydroids are either known as juveniles only or they remain unidentified (Bouillon *et al.*, 2006). Prudkovsky & Neretina (2016) provide list of pandeid species for which the life cycle has been elucidated, usually by rearing experiments (e.g. as described in Rees & Russell, 1937).

Because many species cannot be reared in the laboratory, DNA barcoding has recently been used successfully to link hydroid and medusae stages in different hydrozoan families (Schuchert, 2016; Schuchert *et al.*, 2017 and references therein). The present study continues these studies, focusing here mainly on the pandeid hydroid currently known as *Leuckartiara abyssi* (G.O. Sars, 1874) and its medusa. However, it was also necessary to consider also relationships to other Pandeidae, in particular *Neoturris pileata* and *N. breviconis*.

In 1874, Georg Ossian Sars described *Perigonimus abyssi* (Fig. 1), a tiny new hydroid which he had obtained from two localities in the south-west of Norway (Island of Kvitsøy near Stavanger and the Hardangerfjord near Bergen). Both samples came from relatively deep waters (146-366, resp. and 274-731 m) and they were growing on scaphopods and the bivalve *Nucula tumidula* Malm. Sars noted that the gonophores were rare, but he was quite sure that they would produce a free medusa. As he

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had preserved material only, some uncertainty remained. The species was subsequently recorded from numerous localities in the North Atlantic from Greenland to the Barents Sea (listed in Edwards, 1965). However, all these records must be considered somewhat doubtful (Edwards, 1965) due to the possibility of confusions with other pandeid hydroids, e. g. *Leuckartiara octona* (Fleming, 1823). Most known pandeid hydroids are rather simple and offer few characters to differentiate them, notably in preserved material without gonophores. Rees (1938) then re-sampled living *L. abyssi* hydroids from near Bergen, where it seems to occur quite regularly. Although out of 12 colonies only one had a single gonophore, he was able to follow its development until its release as a young medusa with four tentacles lacking ocelli. This made it distinguishable from *L. octona* medusae which are released with two tentacles only (the ocelli develop later). Rees (1938) concluded that the hydroid is potentially the polyp stage of *Neoturris pileata* (Forsskål, 1775) or any other *Leuckartiara* medusae known from the region. He thus transferred it provisionally to the genus *Leuckartiara* as *L. abyssi*. Later (1956), Rees was able to re-examine the syntype material of which only the colony from Kvitsøy on the scaphopod *Antalis entalis* (Linnaeus) was left. Although with some ambiguity, Rees designated this specimen as the lectotype.

Subsequently, Naumov (1960, 1969) speculated that *L. abyssi* could be the polyp stage of *Catablema vesicarium* (A. Agassiz, 1862). The situation became much clearer when Edwards (1965) documented an identical hydroid growing on *Nucula* shells from the Firth of Clyde (Scotland). Edwards reared the medusae to a stage with well-formed gonadal pits and folds (5 mm height) and he identified it as *Neoturris pileata* based on Russell's (1953) descriptions. Edwards (1965) also found mature *N. pileata* medusae in the plankton of the region, which further supported his identification of the reared medusae. Although Edward's hydroids were indistinguishable from *L. abyssi* polyps from Norway, he refrained from synonymising *L. abyssi* with *N. pileata* because also another *Neoturris* medusa, *N. breviconis* (Murbach & Shaerer, 1902), had been reported from the Bergen region by Kramp & Damas (1925; as *Leuckartiara breviconis*). *Leuckartiara abyssi* could therefore also be the hydroid of *N. breviconis*, a medusa originally described from the NE Pacific Ocean (see Arai & Brinckmann-Voss, 1980; Schuchert, 2007, 2012). Until the re-description by Arai & Brinckmann-Voss (1980), the species was not well known, but several authors reported it also from the North Atlantic, notably the influential Russell (1953) and Kramp (1959). However, most of these records are likely incorrect identifications and at least some refer to other *Leuckartiara*, *Catablema*, and *Neoturris* species (Schuchert, 2007, 2012), notably also *Neoturris pileata*, a very conspicuous and characteristic medusa (Figs 6-7) originally described from the Mediterranean (Forsskål, 1775, 1776). Unambiguous records of *N. pileata* are also known from the North-eastern Atlantic reaching as far north as Scotland, Norway, and Iceland (Hartlaub, 1914; Kramp & Damas, 1925; Kramp, 1926; Russell, 1953; Schuchert, 2007). However, not all individuals are as typical as shown in Fig. 7, some might be smaller or broader (Fig. 6), the apical process can be missing, and the colour of the manubrium is not always as intense as shown in Fig. 7 (Schuchert, 2007). Atlantic *Neoturris pileata* medusae are not always easy to distinguish from *N. breviconis* of the Pacific Ocean (compare Figs 3-7 and 10; see also Schuchert, 2007). The latter species is generally larger, broader, has a less developed apical process, more than 80 tentacles, the manubrium is distinctly shorter and never as red as in *N. pileata*, the gonadal folds are not clearly directed towards interradial and their arrangement resembles more a *Leuckartiara* species.

During several sampling trips in the region of Bergen (Norway), I was able to collect repeatedly *Neoturris* medusae (Figs 3-4) as well as hydroids identifiable as *L. abyssi* (Fig. 2). The *Neoturris* medusae from the Bergen area appeared mature or nearly fully grown (Fig. 4) but were differed somewhat from typical *N. pileata* as found south of the British Isles and in the Mediterrranean (Figs 6-7). It was thus very interesting to use DNA barcoding (Schuchert, 2016; Schuchert *et al.*, 2017) to assess the connection of the polyps and medusae as well as relationships to other Pandeidae species.

Additional Pandeidae species, including also *N. breviconis,* could be obtained for DNA barcoding and observations related *Leuckartiara* and *Catablema* species are also reported in this context.

MATERIAL AND METHODS

Molecular biological methods as well as the sampling of the medusae have already been described in Schuchert *et al.* (2017) and Schuchert (2005, 2012, 2014, 2016). The polyp stages of *N. abyssi* (Table 1) were obtained by sampling molluscs with a modified R-P epibenthic sampler (Rothlisberg & Pearcy, 1976) or a triangular dredge.

The DNA samples are all stored in the DNA collection of the MHNG.

About 600 bp of the large mitochondrial ribosomal RNA (16S) was amplified using the primers SHA (ACGGAATGAACTCAAATCATGT) and SHB (TCGACTGTTTACCAAAAACATA) (Cunningham & Buss, 1993) (30 cycles, profile: 20 sec 94°C, 45 sec 50°C, and 120 sec 68°C).

Fragments of about 660 or 890 bp of the mitochondrial Cytochrome Oxidase I (COI) were amplified using the forward primer COF (TGAGTATTTTCAACTAATCAYAAAGA) combined with either the reverse primers COI3 [TAAACTTCAGGGTGACCAAAAAATCA,

is HCO2198 of Folmer *et al.* (1994)] or CoR (AAGTAAGCTCTAGTATCAACRTCCAT). The PCR cycling profile for the COI fragment was: 5 cycles with 50 sec 94°C, 50 sec 45°C, and 120 sec 70°C; followed by 30 cycles with 50 sec 94°C, 50 sec 50°C, and 120 sec 68°C.

About 750 bp spanning the ITS region of the tandemly repeated ribosomal genes of *Neoturris* and *Catablema* samples was amplified using the primers IFS (GTCGCTACTACCGATTGAATGG) and IRS (CGCTTCACTCGCCGTTACTAGG) (shortened primers of Martinez *et al.*, 2010). The PCR cycling profile for the ITS fragment was: 24 cycles with 20 sec 94°C, 45 sec 51°C, and 90 sec 72°C.

All PCR reactions were done in 50 µl volume using PCR Kits of Qiagen® according to the instructions of the manufacturer. About 1-5 ng of genomic DNA were used as template. The sequencing of the products was made by Macrogen Inc.

The sample data as well as the GenBank numbers of the specimens used in this study are given in Table 1. Some additional Pandeidae 16S and COI sequences which had approximately the same lengths as the ones generated for this study could be retrieved from GenBank (16S sequences JX965913, KT809337, KT809324, KT288206, AM183136, JX965912, JQ715887, JQ715888; COI sequences KT809324, KC440110, GQ120057, KC440107, JQ716057, JX965906, Q716085).

The sequences were edited and aligned using the Bioedit Sequence Alignment Editor (Hall, 1999) and the integrated ClustalW tool with default settings (Larkin *et al.,* 2007). Regions with ambiguous alignments were not removed (removal did not change the results, not shown). Maximum likelihood analyses and substitution model selection were done as given in Schuchert (2016).

Abbreviations:

16S	16S mitochondrial ribosomal RNA gene sequence
BOLD	The Barcode of Life Data System, see Ratnasingham & Hebert (2007)
COI	Cytochrome Oxidase subunit I
DOI	Digital Object Identifier
GenBank	Genetic sequence database of the National Institute of Health, USA http://www.ncbi.nlm.nih.gov/genbank/
ITS	Internal Transcribed Spacer
MHNG	Muséum d'histoire naturelle de Genève, Switzerland

RESULTS AND DISCUSSION

Maximum likelihood analyses

16S and COI sequence data were used to obtain Maximum Likelihood trees (Figs 8-9) that graphically visualise inter- and intraspecific sequence divergences (see also Schuchert *et al.*, 2017). The trees for ITS showed identical relationships for the examined taxa (results not shown).

Neither 16S nor COI resolves satisfactorily the phylogenetic relationships at the genus or family level. However, this was not the aim of this study and will need additional markers like 18S and 28S gene sequences. The aim of the present study was to identify the medusa of *L. abyssi* and concomitantly to evaluate the usefulness of 16S and COI for separating Pandeidae species in barcoding approaches. The 16S, COI, and ITS sequences clearly identified the *Neoturris* medusa from the same locality as the medusa stage of *L. abyssi*. More details are given below.

16S and COI intra- and interspecific variation

The mitochondrial 16S gene sequence tends to be a reliable barcode marker for Hydrozoa and largely replaces the more commonly used COI of other groups because it can be amplified with a higher success rate (Lindsay *et al.*, 2015; Zheng *et al.*, 2014; Schuchert *et al.*, 2017). For the Pandeidae analysed here, however, COI appears more suitable (Table 2, Figs 8-9). The maximal intraspecific sequence divergences range from 0.33% to 0.52% for 16S and 0.9% to 1.68 % for the COI (Table 2). The latter marker has thus about three times greater divergence values. Similarly, the minimal interclade divergences (barcode gaps) tend also to be much higher for COI, resulting in trees with an apparently much better separation of the species clades through longer branches (Fig. 9). The bootstrap values, however, seem not to reflect this, the COI tree has not more supported nodes. The higher divergence of the COI is particularly useful for the *Catablema* species and will be discussed in more detail below.

Neoturris species

Five hydroid colonies of *L. abyssi* from the Bergen area could be obtained to get DNA, all growing on the same organisms as the type material (Fig. 2). Concomitantly, seven *Neoturris* medusae of different ages (sizes) were analysed from the same region (Figs 3-4). They were provisionally named *N. abyssi* after the first DNA sequence comparisons indicated their identity with the hydroid. A single adult medusa of *Neoturris pileata* suitable for DNA extraction could be obtained from the Mediterranean.

The 16S, COI, and ITS sequence data (Figs 8-9) unambiguously associated the polyps *L. abyssi* (Fig. 1-2) with the *Neoturris* medusae shown in Figures 3-4. Some polyp and medusa samples even yielded identical sequences. For both COI and 16S the intraclade divergences were similar to intraspecific variations seen in other Pandeidae (e. g. *N. breviconis*, *L. octona*; Table 2).

Table 1. Sample data, voucher numbers, and GenBank data of specimens examined by the author. The sample data of other sequences retrieved from GenBank and shown in Figs 8-9 can be obtained by searching the accession numbers in GenBank. nd = no data.

species	WGS84 coordinates	locality	depth [m]	date collected	polyp medusa	comments, reference or DOI of photos	MHNG-INVE-voucher	DNA isolate	16S	COI	ITS
Amphinema dinema	48.79717, -3.96817	France, off Roscoff	0-8	30.08.2011	m	typical, mature medusa		887	KP776816	MG136807	nd
Amphinema spec.	41.73520, 2.95412	Spain, Catalonia, Cala Giverola	1-2	11.08.2008	p	typical hydroid for genus		688	MG250194	MG237874	nd
Catablema cf. *multicirratum*	81.36-80.97, 15.25-15.40	north of Svalbard	nd	26.08.2015	m	this study		1139	MG136740	MG136793	MG136766
Catablema cf. *multicirratum*	81.36-80.97, 15.25-15.40	north of Svalbard	nd	26.08.2015	m	this study		1140	MG136741	MG136794	MG136767
Catablema multicirratum	48.54514, -123.01206	USA, San Juan Island	0.5	19.05.2011	m	this study		868	MG136729	MG136781	MG136764
Catablema nodulosum	48.54514, -123.01206	USA, San Juan Island	0	16.05.2011	m	this study		932	MG136727	MG136779	MG136762
Catablema nodulosum	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	this study		957	MG136730	MG136782	MG136765
Halitholus spec.	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	this study		870	MG136735	MG136787	nd
Hydrichthys boycei	nd	South Africa, Durban	nd	July 2005	p	Schuchert (2007)	37417	383	EU448102	MG136811	nd
Leuckartiara cf. *nobilis*	56.455, -5.434	Scotland, Dunstaffnage Bay	0	07.05.2004	m	Schuchert (2007)		299	AM183135	MG136789	nd
Leuckartiara longicalcar	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	this study	78922	869	MG136731	MG136783	nd
Leuckartiara octona	nd	Germany, North Sea	nd	nd	p	Schuchert (2007)	49100	487	AM411422	MG136777	nd
Leuckartiara octona	50.33385, -4.16725	England, Plymouth	0	28.06.2007	m	Schuchert (2007)		564	MG136737	MG136790	nd
Leuckartiara octona	55.035, -1.4286	England, Cullercoats	nd	00.03.2008	p	10.5281/zenodo.896089	63261	734	MG136738	MG136791	nd
Leuckartiara octona	55.035, -1.4286	England, Cullercoats	nd	26.03.2008	p	10.5281/zenodo.896111		721	MG136739	MG136792	nd
Leuckartiara octona	60.275, 5.200	Norway, Raunefjord	10	22.05.2012	m	10.5281/zenodo.896123		915	MG136743	MG136795	nd
Leuckartiara octona	58.25362, 11.39031	Sweden, Gullmarsfjorden	5-50	29.09.2014	p	this study		1055	MG136755	MG136808	nd
Leuckartiara octona	58.24385, 11.43231	Sweden, Kristineberg	0	03.10.2014	m	10.5281/zenodo.896290	89890	1061	MG136756	MG136809	nd
Leuckartiara octona	43.686, 7.317	France, Villefranche-sur-Mer	0-70	04.04.2005	m	10.5281/zenodo.896334		354	AM411421	MG136810	nd
Leuckartiara octonema	34.47806, 136.8675	Japan, Toba City	0	09.05.2014	m	this study	97018	1208	MG136758	MG136813	nd
Leuckartiara spec.	48.54514, -123.01206	USA, San Juan Island	0.5	22.05.2011	m	this study	78921	871	MG136736	MG136788	nd
Neoturris abyssi	60.275, 5.200	Norway, Raunefjord	10	22.05.2012	m	this study		953	MG136742	nd	MG136768
Neoturris abyssi	60.20833, 5.20261	Norway, Korsfjord	0-20	23.05.2012	m	this study	82129	916	MG136744	MG136796	MG136769
Neoturris abyssi	60.20833, 5.20261	Norway, Korsfjord	0-20	23.05.2012	m	this study		917	MG136745	MG136797	MG136770
Neoturris abyssi	60.20833, 5.20261	Norway, Korsfjord	0-20	23.05.2012	m	this study		918	MG136746	MG136798	MG136771
Neoturris abyssi	60.20833, 5.20261	Norway, Korsfjord	0-20	23.05.2012	m	this study		919	MG136747	MG136799	nd
Neoturris abyssi	60.20833, 5.20261	Norway, Korsfjord	0-20	23.05.2012	m	this study		954	MG136748	MG136800	nd
Neoturris abyssi	60.24079, 5.22941	Norway, Fanafjord	0-30	24.04.2015	m	this study		1119	MG136749	MG136801	MG136772
Neoturris abyssi	60.33802, 5.18163	Norway, Raunefjord	32-42	16.09.2008	p	this study		935	MG136750	MG136802	MG136773
Neoturris abyssi	60.33802, 5.18163	Norway, Raunefjord	32-42	16.09.2008	p	this study		936	MG136751	MG136803	nd
Neoturris abyssi	60.30282, 5.2016	Norway, Raunefjord	45-100	19.09.2008	p	this study		694	MG136752	MG136804	MG136774
Neoturris abyssi	60.435, 5.122	Norway, Hauglandosen	135-151	19.09.2008	p	this study	62572	695	MG136753	MG136805	MG136775
Neoturris abyssi	60.435, 5.122	Norway, Hauglandosen	135-151	19.09.2008	p	this study	62572	704	MG136754	MG136806	nd
Neoturris breviconis	48.54514, -123.01206	USA, San Juan Island	0	16.05.2011	m	this study		949	MG136726	MG136778	MG136761
Neoturris breviconis	48.54514, -123.01206	USA, San Juan Island	0.5	19.05.2011	m	this study		882	MG136728	MG136780	MG136763

species	WGS84 coordinates	locality	depth [m]	date collected	polyp medusa	comments, reference or DOI of photos	MHNG-INVE-voucher	DNA isolate	16S	COI	ITS
Neoturris pileata	43.685, 7.31567	France, Villefranche-sur-Mer	0-30	11.04.2017	m	this study	97957	1280	MG136759	MG136814	MG136776
Oceania armata	43.686, 7.317	France, Villefranche-sur-Mer	0	21.01.2014	m	Schuchert (2016)	87094	956	KP776815	KX096599	nd
Pandea conica	43.685, 7.31567	France, Villefranche-sur-Mer	0-30	14.04.2017	m	10.5281/zenodo.896414	97958	1281	MG136760	MG136815	nd
Pandeopsis ikarii	34.47812, 136.867	Japan, Toba City	0	nd	m	this study	92017	1129	MG136757	MG136812	nd
Stomotoca atra	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	10.5281/zenodo.998730		884	MG136732	MG136784	nd
Stomotoca atra	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	this study		960	MG136733	MG136785	nd
Stomotoca atra	48.54514, -123.01206	USA, San Juan Island	0.5	20.05.2011	m	this study		961	MG136734	MG136786	nd

Table 2: Selected clade divergences of 16S, COI, and ITS sequences calculated as p-values in %

Maximal intraclade p-values in % (= intraspecific or intrageneric divergences)			
clades	**16S**	**COI**	**ITS**
Neoturris pileata+abyssi	0.50	1.50	1.32
Neoturris abyssi Norway population	0.50	1.51	1.32
Neoturris breviconis	0.52	1.51	0.0
Leuckartiara octona	0.50	1.68	-
Stomotoca atra	0.33	0.90	-
genus *Catablema*	0.34	3.77	1.31

Minimal p-values in % of selected clade pairs (= interspecific divergences, barcode gaps)			
clades	**16S**	**COI**	**ITS**
Neoturris abyssi Norway vs. *N. pileata*	0.17	0.30	0.0
N. pileata+abyssi vs. *N. breviconis*	2.01	8.89	7.7
L. octona vs. *L.* cf. *octonema*	2.01	8.56	-
L. octona vs. *L. longicalcar*	1.17	5.72	-
Catablema multicirratum vs. *C. vesicaria nodulosum*	0.17	2.41	0.92
A. dinema Atlantic vs. *A. dinema* Pacific	15.1	16.1	-

Most importantly, however, the sequences placed the Mediterranean sample of *N. pileata* clearly within this *L. abyssi* clade, this with very little sequence divergence. The sequence differences of the *N. pileata* sample to *N. abyssi* are smaller than the maximal intrapopulation differences of *Neoturris abyssi* (Figs 3-4, Table 2). This is thus good evidence that *L. abyssi* is conspecific with *N. pileata*. Therefore, despite the morphological differences (compare Figs 3-6; colour of manubrium, bell-size, and proportion of height to width), the genetic data confirm the suspicion of Edwards (1965) that both are conspecific. Edwards (1965) hesitated to synonymise the two names because also another *Neoturris* medusa, *N. breviconis* (Murbach & Shaerer, 1902), had been reported from the North Sea by Hartlaub (1914) and later by Kramp & Damas (1925; as *Leuckartiara breviconis*) for the Bergen region. *Neoturris breviconis* was originally described from the NE Pacific (Fig. 10) and until the re-description of Arai & Brinckmann-Voss (1980) it was not well known and misidentified by a number of authors. The Atlantic animals depicted by the influential Russell (1953) and Kramp (1959) were clearly not *N. breviconis.* Re-examination of part of their material showed it to belong to other *Leuckartiara*, *Neoturris*, and *Catablema* species (Schuchert, 2007, 2012). The *Neoturris abyssi* medusae of this study observed near Bergen mostly lacked a distinct apical process, which is often very variable in Pandeidae. The medusae observed by Kramp & Damas (1925) in the same region and identified as *Leuckartiara breviconis* were likely the same and the insignificant apical process may have prompted them to separate them from their *N. pileata* originating from Iceland and the North Sea. True *Neoturris breviconis* originating from the NE Pacific (Fig. 10) appear quite distinct from typical *N. pileata* (Figs 3-6), but the diagnostic differences are much more difficult to formulate, in particular also criteria that can be used for preserved material (see below in Taxonomy section). The molecular data, however, clearly separate the two species (Figs 8-9, Table 2).

The differences (colour, size) of the *Neoturris* medusae from Norway and the Mediterranean observed in the present study are thus likely primarily due to age differences for the size and form, and environmental conditions for the colour differences (primarily the consumed food). A *Neoturris* medusa from Sweden (Fig. 5) had a much darker manubrium, despite being not much larger than the Norwegian ones. The developmental stages documented by Edwards (1965) agree nicely with these observations and also Hartlaub (1914), Russell (1953), and Schuchert (2007) mentioned the high degree of variability of the medusa. Hartlaub (1914) found that the apical process can be well developed but also lacking, the proportion of the manubrium length to bell-height is also very variable, like the number of tentacles (see also Kramp, 1926).

The medusae observed in Norway (Figs 3-4) with sizes of 8-12 mm had not attained the adult size of typical *N. pileata* (2-4 cm, Figs 5-6). Gametes (oogonia) could only be found in the folds of larger medusae (>10 mm, the eggs in mature Mediterranean specimens are also not so easy to observe, they are quite small with a diameter of about 60 µm). In the Mediterranean, juvenile medusa stages have rarely been documented, but those shown in Hartlaub (1914) correspond well to the ones from Norway shown here (Fig. 3). Mediterranean polyps of *N. pileata* are even more rare, having only been reported by Bavestrello (1985). Contrary to the Atlantic counterparts, they were not found on *Nucula* species or scaphopods, but on shells of the hermit crab *Paguristes oculatus* (Fabricius) [now accepted as *Paguristes eremita* (Linnaeus)].

Although the 16S and COI sequence data unambiguously link *L. abyssi* from Norway and *Neoturris pileata* from the Mediterranean, these results depend to some degree on the reliability of these markers to distinguish biological species. While so far they proved to be very reliable for other hydrozoan groups (see Schuchert, 2016; Schuchert *et al.*, 2017 and references therein), the 16S results obtained in this study for three nominal *Catablema* species showed very little divergences, in part less than the maximal intraspecific divergence of other Pandeidae (Table 2, Fig. 8). This apparently puts into question to some degree the general usefulness of 16S as barcoding marker. However, as explained in the next section, the problem is more likely founded in the problematic identifications of the *Catablema* species and to a lesser degree the 16S marker.

Catablema species

16S and COI Sequences of all three currently accepted *Catablema* species could be analysed. The identification details of the new material are given below in the Taxonomy section, but the general results and interpretations must also be discussed in the context of the *Neoturris* section above. In addition to the two forms sequenced for this study, a few sequences of *C. vesicarium* from GenBank were also available and which are derived from correctly identified material (see Taxonomy section).

The surprising result was that the 16S sequences of all three morphotypes had very little sequence variation (Fig. 8), being in the range of intraspecific divergences of other species of the family (Table 2). COI has about three times higher divergence values than 16S (Table 2) and for this marker more structure is seen in the tree (Fig. 9). The Pacific *Catablema multicirrata* as well as the Svalbard *C. multicirrata* diverge clearly from the rest of the sampled specimens, but nevertheless do not reach minimal interspecific values seen for other species pairs (Table 2). The ITS data were similar (not shown).

These results could be used as an argument that 16S is not a suitable DNA barcoding marker for the Pandeidae as some species might not be separated into distinct

clades. However, the problem here seems more likely due to the taxonomy of the *Catablema* species than the 16S marker. As argued in the Taxonomy section, *Catablema nodulosa* is likely only a form of *C. vesicarium* with fewer tentacles. It is well possible that also the medusa identified here as *C. multicirrata* is in fact only a large form of *C. vesicarium* with a high number of tentacles. To conclude, the low divergences of the *Catablema* samples cannot be a priori used to question the value of the molecular data and results linking and synonymising of *N. abyssi* and *N. pileata*.

TAXONOMY

Remarks: Some of the material listed in Table 1 and used for the phylogenetic trees in Figures 8-9 has already been described in Schuchert (2007). Only pandeid species for which new information or interpretations have become available are discussed here.

Genus *Neoturris* Hartlaub, 1914

Type species: *Medusa pileata* Forsskål, 1775 (Kramp, 1959).

Remarks: For the diagnosis see Schuchert (2007). The genus comprises the species *Neoturris pileata* (Forsskål, 1775); *N. breviconis* (Murbach & Shaerer, 1902); *N. papua* (Lesson, 1843); *N. bigelowi* Kramp, 1959; *N. crockeri* Bigelow, 1940; *N. fontata* (Bigelow, 1909a); *N. pelagica* (Agassiz & Mayer, 1902). The first three are well described species, the others all need to be redescribed and some of them are rather doubtful.

Neoturris pileata (Forsskål, 1775)

Figs 1-7

Medusa pileata Forsskål, 1775: 110. – Forsskål, 1776: pl. 33, fig. D.
Oceania Lesueurii Péron & Lesueur, 1810: 345. – Goy, 1995: 244, plate.
Carybdea pisifera Oken, 1815: 125.
Oceania pileus de Blainville, 1830: 258.
Oceania ampullacea M. Sars, 1835: 22, pl. 4 fig. 8. – Haeckel, 1879: 58, synonym.
Tiaria papalis Lesson, 1843: 287. – Haeckel, 1879: 58, synonym.
Turris digitale Forbes, 1846: 286. – Hartlaub, 1914: 324, synonym.
Turris digitalis. – Forbes, 1848: 21, pl. 3 fig. 1. – Haeckel, 1879: 61, pl. 4 figs 2-3. – Kramp, 1955: 153, revision of Haeckel's material.
Oceania episcopalis Forbes, 1848: 27, pl. 2 fig. 1. – Haeckel, 1879: 58, synonym.
Oceania coccinea Leuckart, 1856: 20, pl. 2 fig. 3.– Haeckel, 1879: 58, synonym.
Oceania constricta Patterson, 1859: 279, figs.
Tiara pileata. – Haeckel, 1879: 58, pl. 3 figs 6-8.
Turris coeca Hartlaub, 1892: 19, fig. 1. – Hartlaub, 1914: 329, synonym.
in part *Turris pileata.* – Mayer, 1910: 123, pl. 12 fig. 4, pl. 13 fig. 6.
Tiara pileata. – Le Danois, 1914: 17, fig. 4.
Perigonimus abyssi G.O. Sars, 1874: 126, pl. 5 figs 27-30. **new synonym**
Neoturris pileata. – Hartlaub, 1914: 326, figs 270, 273, 274-281. – Kramp, 1926: 92, fig. 37, pl. 2 figs 13-14, chart XVIII. – Russell, 1953: 203, figs 104-106, pl. 12 fig. 1. – Edwards, 1965: 461, figs 1-4, life cycle. – Schuchert, 2007: 333, figs 59-60, review.
in part *Leuckartiara brevicornis.* – Hartlaub, 1914: 304, figs 254-256. [incorrect subsequent spelling]
in part *Leuckartiara breviconis.* – Kramp, 1926: 80, pl. 2 fig. 8. – Russell, 1953: 198, pl. 12 fig. 2. – Kramp, 1959: 120, fig. 121. [not *Neoturris breviconis* (Murbach & Shaerer, 1902)]
Leuckartiara breviconis. – Kramp & Damas, 1925: 280 [not *Neoturris breviconis* (Murbach & Shaerer, 1902)]
Leuckartiara abyssi. – Rees, 1938: 19, fig. 6a-d, part of life cycle. – Rees, 1956: 114, re-examination of type material, lectotype designation. – Schuchert, 2007: 330, fig. 57, redescription, status.

Type locality: Mediterranean

Material of *N. abyssi*: All specimens came from Bergen area in Norway. See also Table 1 for GenBank numbers. If no museum accession number is given, there is no material in a permanent collection.
Hydroid stage:
MHNG-INVE-54693; without gonophores on *Nucula* spec; Herdlafjord, 60.503° 5.2152°, 375-440 m depth; collection date 20.04.2007. – MHNG-INVE-54695;

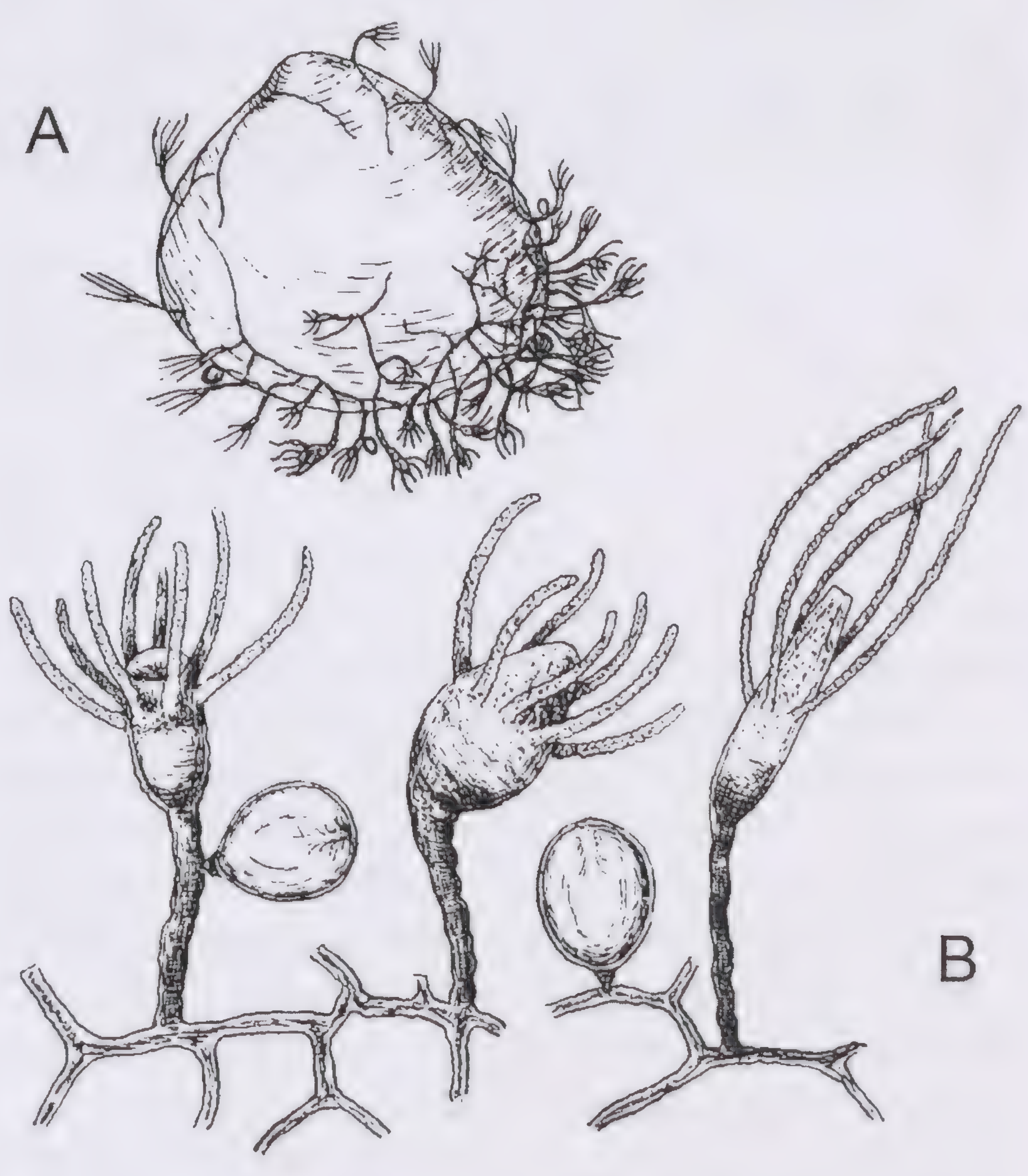

Fig. 1. *Neoturris abyssi*, original illustration of Sars (1874).

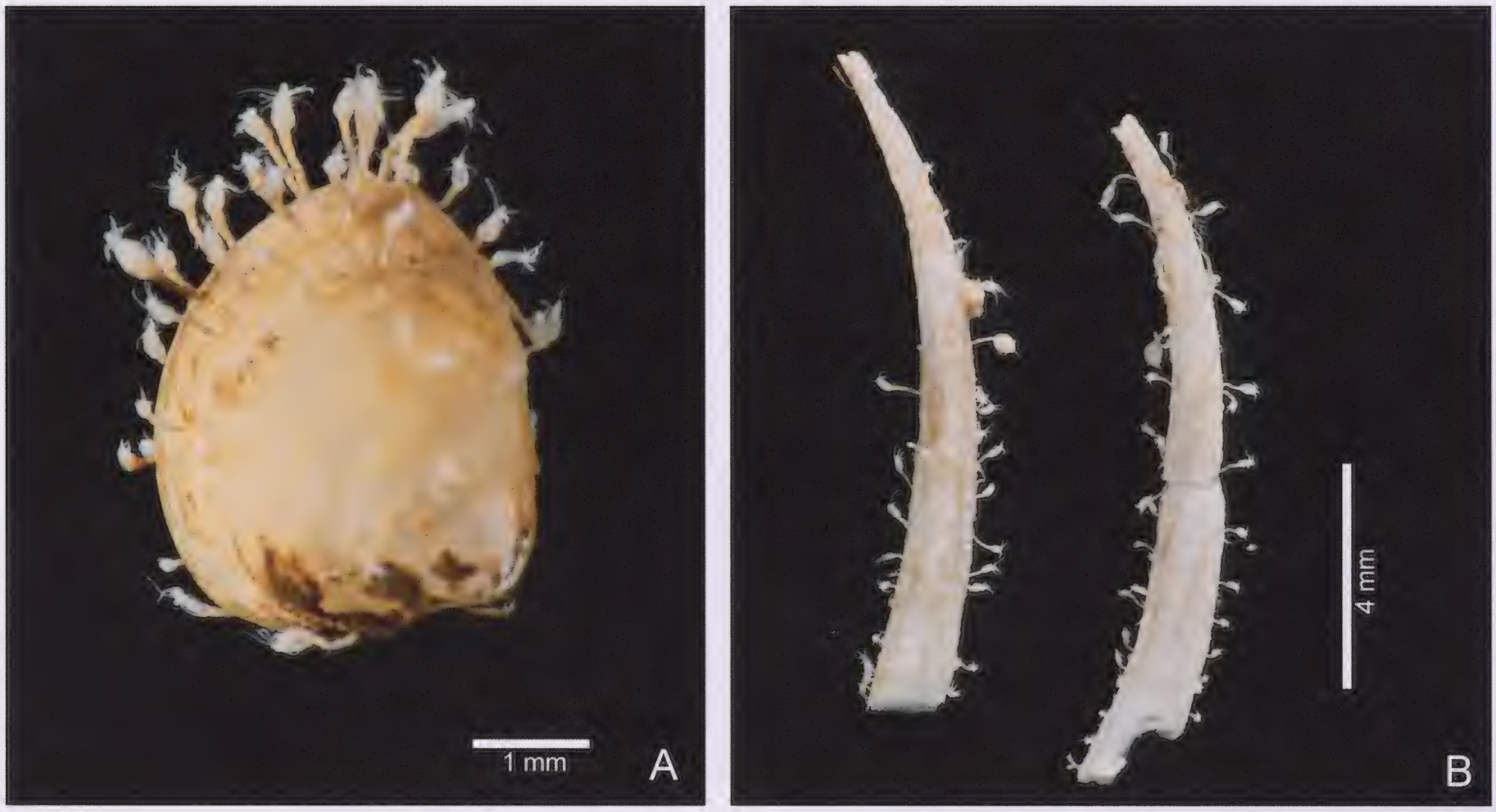

Fig. 2. *Neoturris abyssi* (=*Neoturris pileata*), preserved polyp specimens from Norway, Bergen area, Hauglandsosen. (A) MHNG-INVE-54695 on *Nucula* spec. (B) MHNG-INVE-62572, on a scaphopod, (DNA 695, see Table 1).

without gonophores on *Nucula* spec.; Hauglandsosen, 60.433°5.1167°, 180 m depth; collection date 15.08.2007. – Hydroid without gonophores on scaphopod of about 5 mm size; Raunefjord, Vatlestraumen, 60.33802° 5.18163°, 32-42 m depth; collection date 16.09.2008; DNA isolate 935. – Hydroid without gonophores on *Nucula* spec.; Raunefjord, Vatlestraumen, 60.338017° 5.181633°, 32-42 m depth, temperature °C; collection date 16.09.2008; DNA isolate 936. – Hydroid without gonophores on sipuncule in *Antalis entalis*; Raunefjord, Flesland, 60.30282° 5.2016°, 45-100 m depth; collection date 19.09.2008; DNA isolate 694. – Hydroid without gonophores on *Nucula* spec; Hordaland, Hauglandosen, 60.435° 5.122°, 135-151 m depth; collection date 19.09.2008; DNA isolate 695. – Hydroid without gonophores on *Nucula* spec; Hordaland, Hauglandosen, 60.435° 5.122°, 135-151 m depth; collection date 19.09.2008; DNA isolate 704.
Medusa stage:
Raunefjord, 60.275° 5.200°, 10 m depth; collection date 22.05.2012; DNA isolate 953. – MHNG-INVE-82129; Korsfjord, 60.20833° 5.20261°, 0-20 m depth; collection date 23.05.2012; DNA isolate 916. – Korsfjord, 60.20833° 5.20261°, 0-20 m depth; collection date 23.05.2012; DNA isolate 917. – Korsfjord, 60.20833° 5.20261°, 0-20 m depth; collection date 23.05.2012; DNA isolate 918. – Korsfjord, 60.20833° 5.20261°, 0-20 m depth; collection date 23.05.2012; DNA isolate 919. – Korsfjord, 60.20833° 5.20261°, 0-20 m depth; collection date 23.05.2012; DNA isolate 954. – Fanafjord, 60.24079° 5.22941°, 0-20 m depth; collection date 24.04.2015; DNA isolate 1119.

Material of *N. pileata*: MHNG-INVE-97957; France, Bay of Villefranche-sur-Mer, 43.685° 7.315667°, 0-30 m depth; collection date 11.04.2017; DNA isolate 1280. Additional examined material is given in Schuchert (2007).

Diagnosis: *Neoturris* medusa with bell that is usually higher than wide, height 2-4 cm, no exumbrellar nematocyst ridges, with or without apical projection, no apical canal, with up to 60-90 tentacles. Manubrium usually longer than half the subumbrella height, interradial gonad region large and without folds but with many gonadal pits (>20 per quadrant), eight adradial rows of horizontal gonads folds, folds appear directed towards interradii; no papillae on gonads, radial canals jagged, tentacle bases without abaxial spurs, no ocelli. Colours depending on age and environment, manubrium in younger ones yellow-orange, in fully grown medusae pink to ruby-red; tentacle-bases yellowish.
Hydroids usually on scaphopods and *Nucula* shells, colonial, arising from creeping stolons; hydrocauli covered by perisarc, not branched, monosiphonic. Perisarc extends onto hydranth body as a more or less gelatinous pseudohydrotheca which does not envelop the tentacles. Hydranths with conical hypostome, one whorl of filiform tentacles. Gonophores develop on cauli or stolons, enclosed in thin perisarc membrane. Gonophores liberated as free medusae with four tentacles.

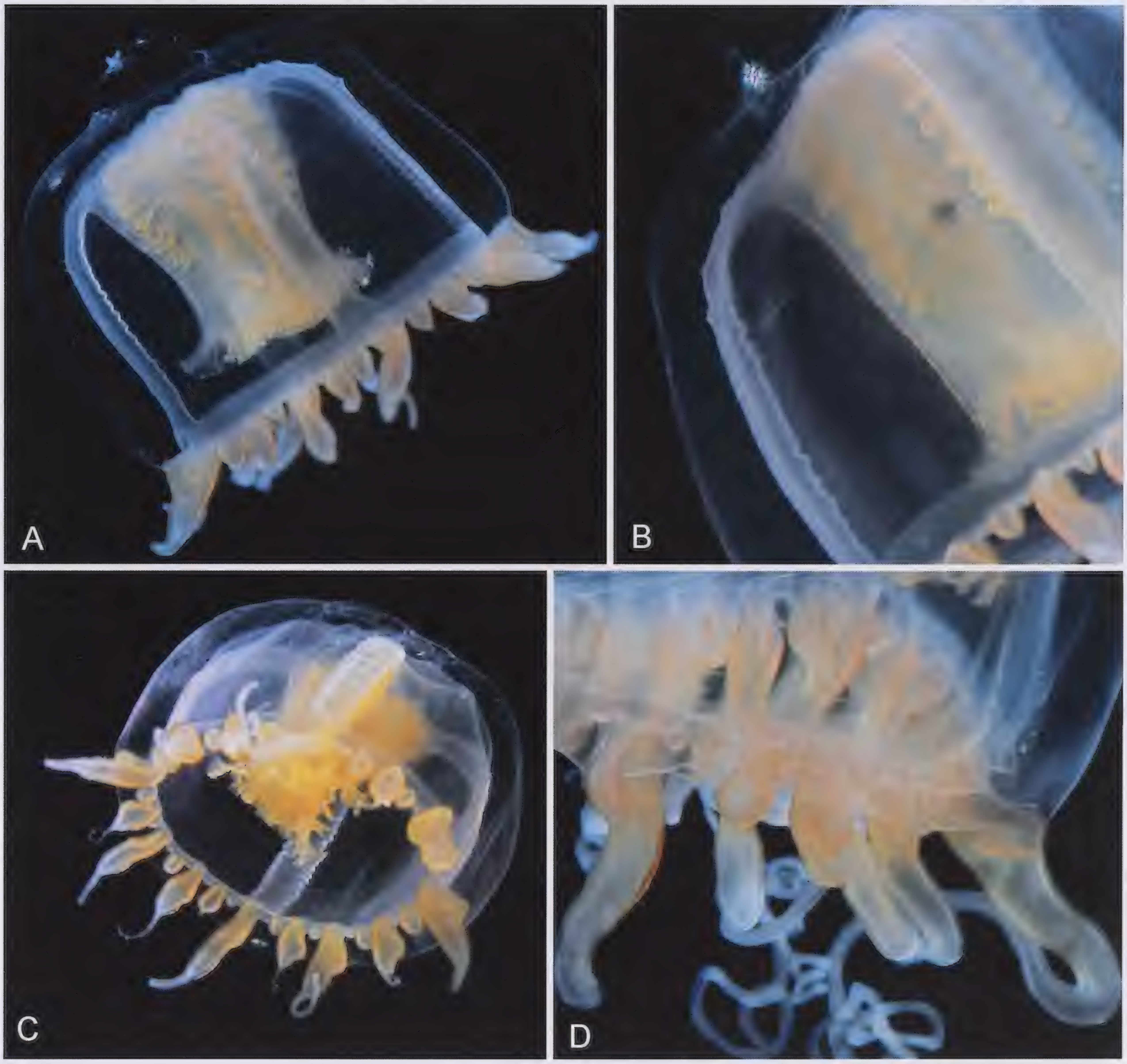

Fig. 3. *Neoturris abyssi* (=*Neoturris pileata*) medusae from Norway, photographs of living, relatively young stages. (A) Lateral view of medusa with bell size 7 mm (DNA 953, see Table 1). (B) Same as A, detail of radial canals and folds of stomach wall. (C) Same as A, oblique view from below. (D) Animal of bell size 9 mm, detail of tentacle bases, note the absence of ocelli.

Description: See Schuchert (2007).

Remarks: As already suspected by Edwards (1965), the 16S and COI sequence comparisons presented above are evidence that the hydroid *Leuckartiara abyssi* G.O. Sars, 1874 must belong to *Neoturris pileata* (Forsskål, 1775). The hydroid of *L. abyssi* from near the original collecting site of Sars belongs unambiguously to *Neoturris* medusae found at the same locality. These *Neoturris* medusae were smaller than those of adult Mediterranean ones (largest ones seen about 15 mm high), but the morphology of the manubrium with its numerous interradial pits and the adradial folds (Fig. 4B) comes close to the ones in more southern waters (comp. Figs 6-7). The colour of the manubrium was, however, never as red as found in medusae south of Norway to the Mediterranean. A *Neoturris* medusa from Sweden (Fig. 5) had a much darker manubrium, despite being not much larger than the Norwegian ones. The yellowish *Neoturris* medusae occur regularly in the Bergen region (see also Hosia & Båmstedt, 2007; as *N. pileata*) and must also have been seen by Kramp & Damas (1925) who attributed them to *N. breviconis*. The sequence comparison made here (Figs 8-9), however, show that this cannot be the case as *N. breviconis* is well separated from the *N. abyssi*+*N. pileata* clade.

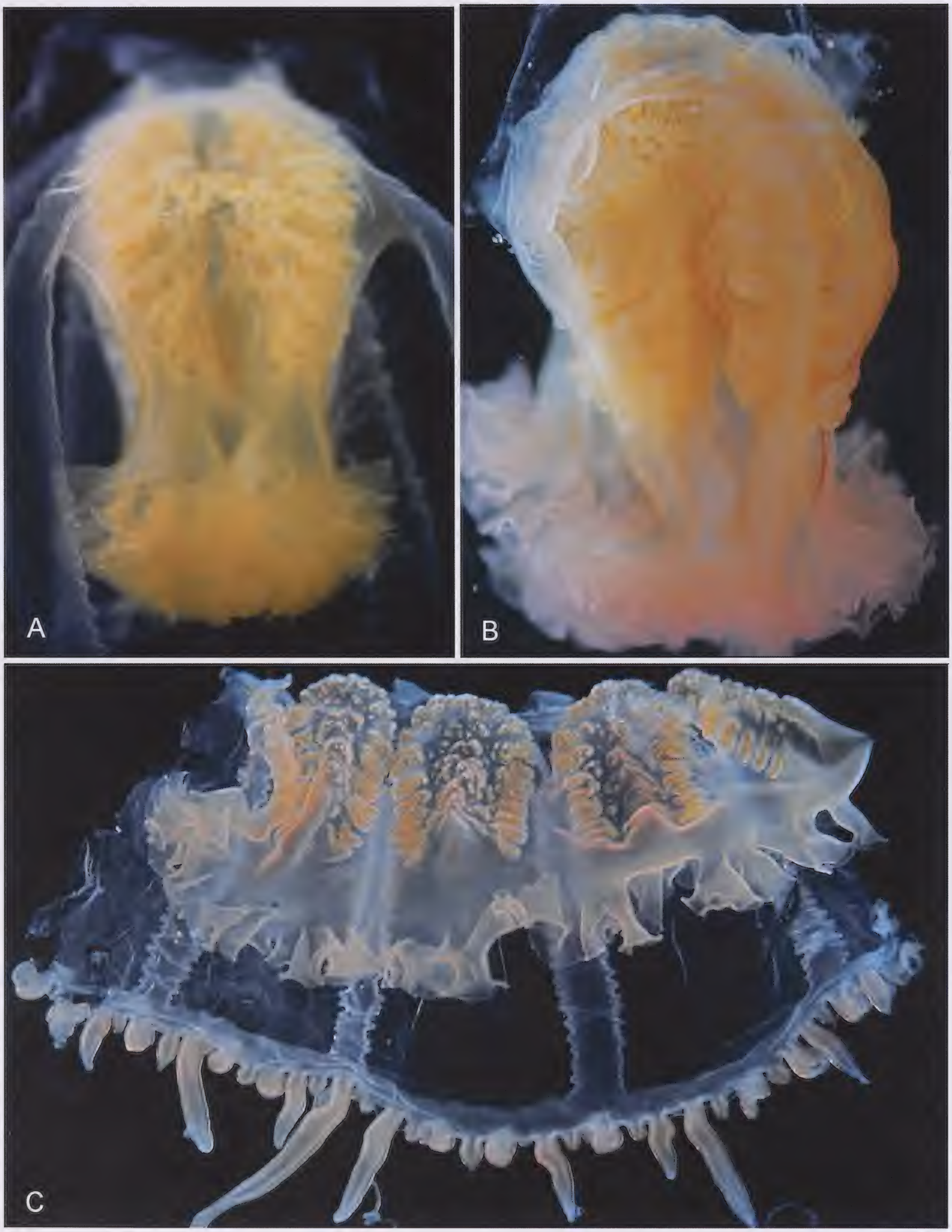

Fig. 4. *Neoturris abyssi* (=*Neoturris pileata*) medusae from Norway, photographs of the most advanced stages found. (A) Lateral view of manubrium of a medusa with bell size 9 mm (DNA 918, see Table 1). No gametes could be seen when examining the gonad fold under a compound microscope. (B) Manubrium of a medusa with bell size 12 mm (DNA 916, see Table 1); note the increased number of gonadal folds and pits. Small oocytes were present in the gonads folds. Except for the colour this animal closely resemble Mediterranean specimens (Figs 6-7). (C) Medusa of about 10 mm height (DNA 919, see Table 1) cut open and spread to visualise anatomical details (inner side of stomach facing observer).

Fig. 5. *Neoturris abyssi* (=*Neoturris pileata*), living medusa from the Swedish coast, photo taken by Fredrik Pleijel and reproduced with the permission of the author. The manubrium is contracted, feigning a horizontal gonadal fold on the manubrium resembling the permanent one seen in some *Leuckartiara* species. This photo is copyright protected and it must not be reproduced without the consent of the author.

Fig. 6. *Neoturris pileata*, preserved specimen (MHNG-INVE-35522) from the Mediterranean, collected before 1895 and identified by C. Hartlaub. Note that the bell shape is not elongated as often seen in other illustrations (e.g. Fig. 7), but nevertheless lies within the range of variation for Mediterranean specimens. Moreover, the bell is somewhat flattened in this preserved sample.

The hydroid of *N. pileata* without medusa buds is not readily distinguishable from *Leuckartiara octona,* the only other pandeid known from the region (Hosia & Båmstedt, 2007). The only character to reliably distinguish the two is found in the newly released medusae, which have four tentacles instead of the two tentacles present in *L. octona*. A less reliable character is the absence of branching of the stems, which in fully grown colonies of *L. octona* are quite regularly branched once, but not so in *N. abyssi.* The Norwegian hydroids here assigned to *L. abyssi* lacked medusa buds, but were nevertheless assigned to *L. abyssi* because they came from close to the type locality, they grew on the typical substrate, the pedicels were never branched, and they occurred in relatively deep waters. Their sequences separated them immediately from *L. octona* medusae collected at the same locality (Figs 8-9). An infertile pandeid hydroid on a *Nucula* shell collected in 5-50 m depths along the Swedish coast (DNA 1055, Table 1) was initially also identified as *L. abyssi*, but the DNA data clearly identified it as *L. octona* and it was reclassified accordingly.

Neoturris breviconis (Murbach & Shaerer, 1902)
Fig. 10A-E

Turris breviconis Murbach & Shearer, 1902: 73. – Murbach & Shearer, 1903: 170, pl. 18 figs 1-2. – Mayer, 1910: 127.

in part *Leuckartiara brevicornis*. – Hartlaub, 1914: 304, figs 254-256. [subsequent incorrect spelling]

not *Leuckartiara breviconis*. – Kramp & Damas, 1925: 280. [= *Neoturris pileata* (Forsskål, 1775)]

in part or not *Leuckartiara breviconis*. – Kramp, 1926: 80, pl. 2 fig. 8. – Russell, 1953: 198, pl. 12 fig. 2. – Kramp, 1959: 120, fig. 121. – Kramp, 1961: 103. – Kramp, 1968: 4, fig. 124. – Russell, 1970: 246.

not *Perigonimus breviconis*. – Naumov, 1969: 204, fig. 72. [= *Catablema multicirratum*]

Neoturris breviconis. – Arai & Brinckmann-Voss, 1980: 57, figs 31-33, new combination.

in part *Neoturris breviconis*. – Schuchert, 2007: 338, fig. 61A-B, not 61C-E.

Type locality: St. Paul Island, Pribilof Islands, Bering Sea.

Material examined: MHNG-INVE-82207, 1 mature specimen in ethanol; Canada, Vancouver Island, 49.0.467°-124.5018°, 0 m depth; collection date 21.05.2012; leg. M. Galbraith. – Several specimens,

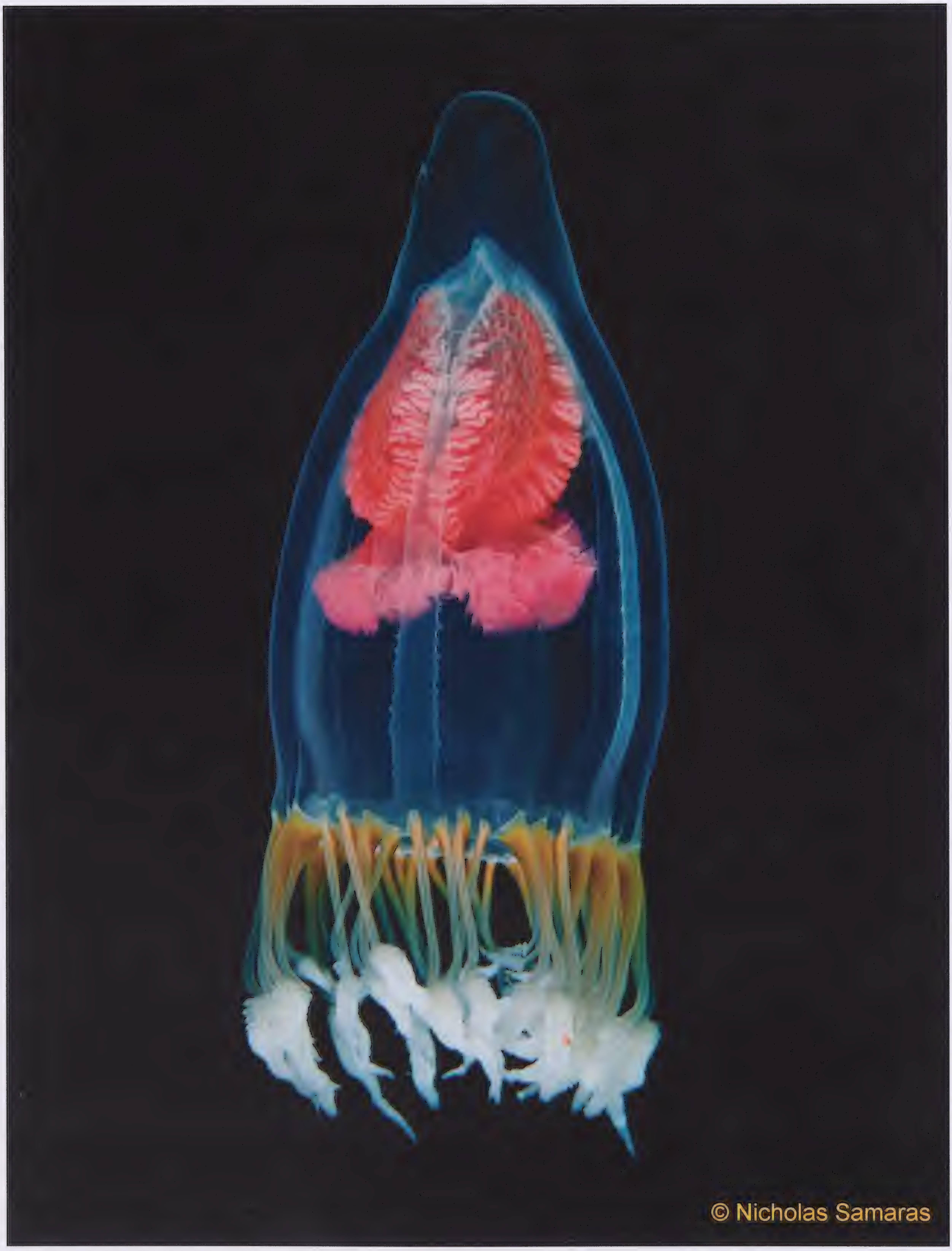

Fig. 7. *Neoturris pileata*, living medusa photographed by Nicholas Samaras, location: Mediterranean, Greece, Chalkidiki Peninsula, depth 3 m. The photo shows a perfect and typical *N. pileata*, note the intense red colour of the manubrium as well as the folds and pits on it. Note that this photo is copyright protected and the right to reproduce it here was acquired by paying a royalty fee to the copyright holder Nicholas Samaras (www.underwater-photography.gr).

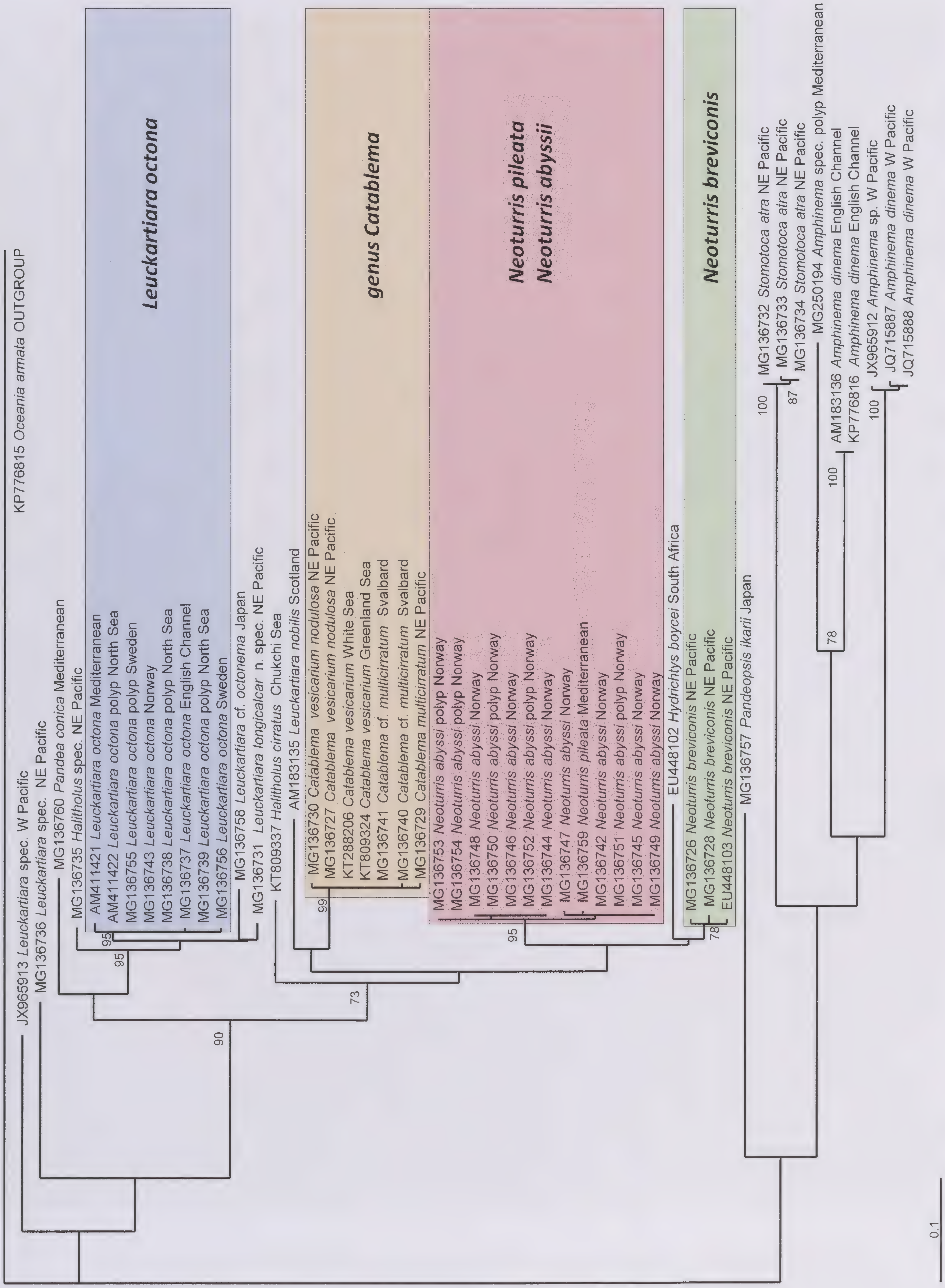

Fig. 8. 16S maximum likelihood phylogenetic tree of Pandeidae species obtained with PhyML (GTR+G+I model) and based on 595 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Table 1.
Samples based on the polyp stage are indicated, all others are medusa samples.

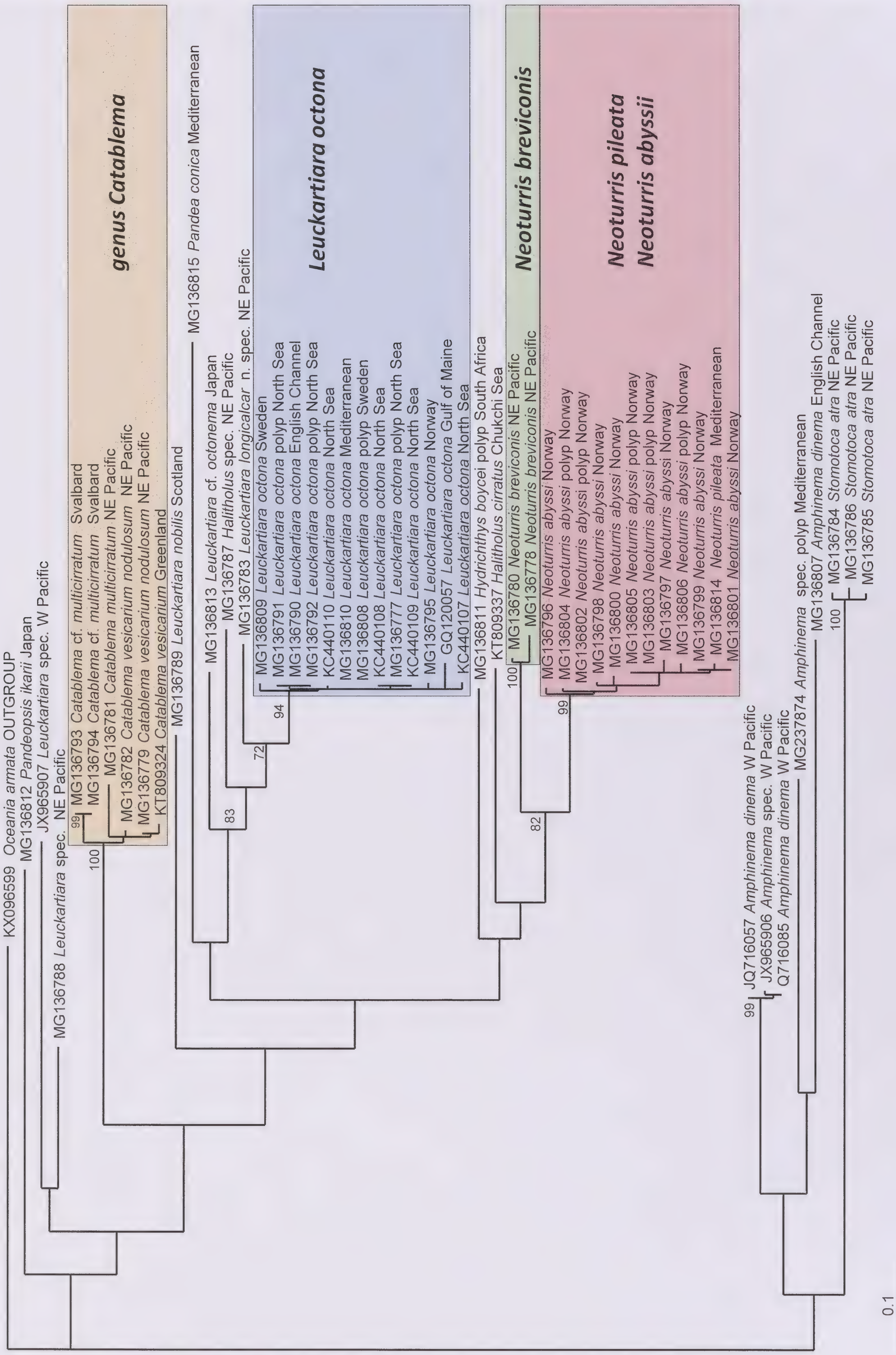

Fig. 9. COI maximum likelihood phylogenetic tree of Pandeidae species obtained with PhyML (GTR+G+I model) and based on 664 bp positions of the mitochondrial COI gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Table 1.
Samples based on the polyp stage are indicated, all others are medusa samples.

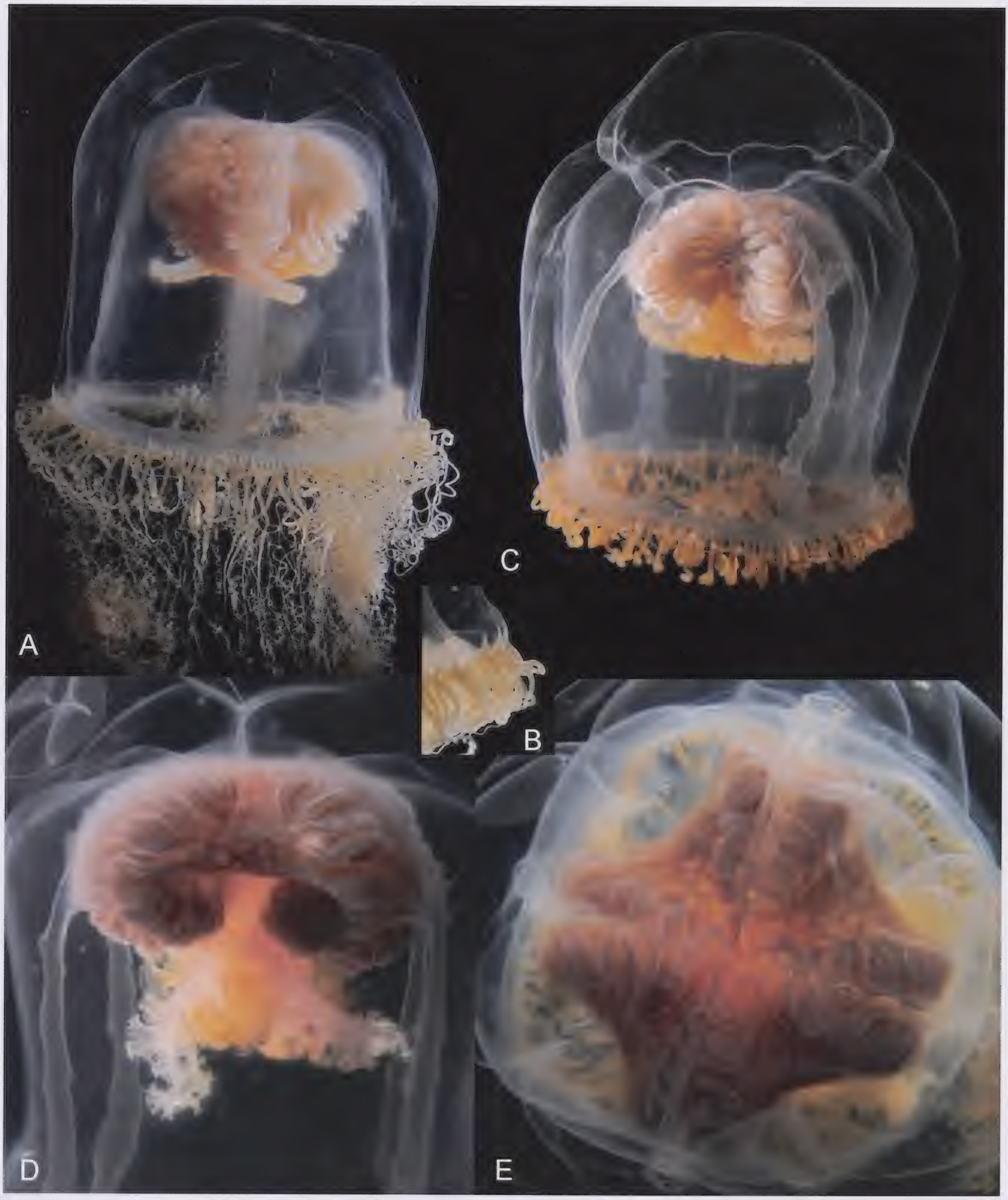

Fig. 10. *Neoturris breviconis,* living individuals from Friday Harbor, USA. (A) Fully grown animal without apical process, height approximately 3-4 cm. (B) Tentacle bases, note abaxial spurs and the absence of ocelli. (C) Smaller animal than shown in A (not to scale) with an apical process. (D) Medusa of with dark pigment in gonad region. The H-form of the gonad-bearing part of the manubrium is rather characteristic, but only temporary as due to contraction. This H-shape of the gonads is reminiscent of some *Leuckartiara* species. (E) Same specimen as in D seen from aboral side. Note that the gonadal pits are more numerous and much better seen in this view.

not in permanent collection; USA, San Juan Island, Friday Harbor, 48.54514°-123.01206°, 0-0.5 m depth, collection date 16.05.2011; DNA isolates 949 and 882, photos Fig. 10, see also Table 1.
Presumed Atlantic material was examined for the publication Schuchert (2007).

Diagnosis: *Neoturris* medusa up to 45 mm high, broad, cylindrical bell, without or with shallow apical process, no exumbrellar ridges with nematocysts, manubrium voluminous, about half or less the height of subumbrella, 90-140 tentacles of similar size, interradial gonad region with 5-20 pits per quadrant, no papillae on gonads, radial canals jagged. Manubrium orange-brown sometimes with dark pigment granules at surface of gonads.

Description: Medusa up to 45 mm high and 35 mm wide, bell often rather cylindrical, top evenly rounded or with a shallow apical projection. Without exumbrellar ridges with nematocysts. Apical canal above manubrium absent or very thin. Aboral subumbrella often with distinct interradial pockets.
Manubrium broad and voluminous, about half the height of subumbrella or less; mesenteries variable in length, usually 1/3 of manubrium height; mouth margin crenulated or finely folded, perradial corners of often drawn out into long processes (Fig. 10A, D). Gonad tissue in upper two thirds of manubrium wall, this region with rows of horizontal folds along the radial canals, about 20 such folds per row, folds thick, and somewhat irregular, some also branched, most folds do not appear directed towards interradial (only those close to top, Fig. 10E), interradial region of gonads rather narrow and depressed, with 5-20 pits per quadrant. If disturbed, the animal can contract the manubrium, resulting in a temporary horizontal fold that looks like a connection of the gonad-folds as seen in the genus *Leuckartiara* (Fig. 10D).
Radial canals jagged and very broad. Ring canal smooth, broad. Up to 140 tentacles, densely crowded, no rudimentary tentacles but some smaller tentacles in development. Marginal tentacle bulbs elongated, laterally compressed conical and tapering rapidly, base grasping margin with or without abaxial spur (Fig. 10B), no ocelli. Tentacles without permanent row of folds.
Color of living specimens, gonads and manubrium pale orange-brown, surface of gonads sometimes with dark red to purple pigment granules (Fig. 10D-E).
Younger animals with short gonad-zone, low number of shallow folds, few interradial pits (figures 31-32 in Arai & Brinckmann-Voss (1980).
Hydroid not known.

Remarks: When describing *N. breviconis*, Murbach & Shearer (1903) already noted the similarity of this species to *N. pileata*, but the illustration depicting the medusa seen from the side was somewhat inaccurate and they did not mention the interradial pits. In his revision of the Pandeidae, Hartlaub (1914) deplored these inaccuracies, but hesitatingly also attributed some badly preserved medusae from the northern North Sea to this species. His specimens were smaller (23 mm in height) and the gonad folds resembled more the ones in the genus *Leuckartiara*. Therefore, he introduced the new combination *Leuckartiara breviconis* (Murbach & Shaerer, 1902). There were no ocelli present, but his material had been preserved for a long time and the pigment of ocelli disappears after a few months in formalin. Later, also Kramp (1926, 1959) and Russell (1953) thought to have found Atlantic specimens of this species. Their illustrations, however, were not *N. breviconis*. Schuchert (2007, 2012), after re-examination of some of Hartlaub's and Kramp's medusae, found that they are unlikely *N. breviconis*, perhaps rather large *Leuckartiara nobilis,* other *Neoturris,* or *Catablema* species.
After examination of medusae from the NE Pacific, Arai & Brinckmann-Voss (1980) found that the species closely resembles *N. pileata* (gonad structure, absence of ocelli) and they transferred it from the genus *Leuckartiara* to the genus *Neoturris*.
Living *Neoturris breviconis* originating from the NE Pacific (Fig. 10) look quite distinct from typical *N. pileata* (Figs 3-6), but the diagnostic differences are much more difficult to formulate, in particular also criteria that can be used for preserved material. *Neoturris breviconis* can be distinguished from *N. pileata* by the broader shape of the exumbrella, the relatively short manubrium, the smaller number of interradial pits on the manubrium (5-20 versus > 20 per quadrant), and the higher number of tentacles (fully grown 90-140 tentacles versus 60-80). Additionally, the apical projection if present is smaller, the adradial gonadal folds not clearly directed towards interradii (except the most aboral ones), and the tentacles bases may have short abaxial spurs. The 16S and COI sequence data clearly separate *N. pileata* and *N. breviconis* (Figs 8-9).
While it is well possible that *N. breviconis* is also present in the Atlantic, currently available evidence is insufficient to establish its presence in the Atlantic. New, living samples must be examined and ideally also their 16S or COI sequences compared with the data presented here.
There exist a few other, little known Pacific *Neoturris* species which are best distinguished using Kramp (1968).

Genus *Catablema* Haeckel, 1879

Type species: *Turris vesicaria* A. Agassiz, 1862 (Kramp, 1959).

Remarks: For the diagnosis see Schuchert (2007). The genus currently comprises the species *Catablema vesicarium* (A. Agassiz, 1862), *C. multicirratum* Kishinouye, 1910, and *C. nodulosum* Bigelow, 1913. According to Hartlaub (1914), Kramp (1959, 1961, 1968), Arai & Brinckmann-Voss (1980), and Schuchert (2007), the three can be distinguished as follows,

characteristics that were also used to identify the present material:

C. vesicarium – up to 32 tentacles, rarely 48, bell size up to 3 cm, in North Atlantic and Arctic Sea

C. nodulosum – 8 to 16 tentacles, bell-size up to 2 cm, in North Pacific

C. multicirratum – 80 to 160 tentacles, bell size up to 6 cm; in North Pacific and Arctic Sea.

Catablema vesicarium (A. Agassiz, 1862)

? *Medusa campanula* Fabricius, 1780: 366.

Catablema campanula. – Haeckel, 1879: 63, pl. 4 figs 4-5. – Kramp, 1955: 153, re-examined material of Haeckel.

Turris vesicaria A. Agassiz, 1862: 97. – Agassiz, 1865: 164, figs 261-268.

in part *Turris vesicaria*. – Mayer, 1910: 126, pl. 12 figs 2-3 (not pl. 13. fig. 7 = *L. octona*).

Catablema vesicarium. – Bigelow, 1909b: 304, pl. 30 figs 3-4, pl. 31 fig. 6. – in part Hartlaub, 1914: 315, figs 263-267. – Kramp, 1926: 87, pl. 2 figs 10-11. – Kramp 1959: 122, 208-212, fig. 125. – Kramp, 1961: 96. – Kramp, 1968: 50, fig. 132. – Schuchert, 2007: 345, fig. 64, redescription. – Prudkovsky & Neretina, 2016: 533, figs 1-8, life cycle.

Catablema eurystoma Haeckel, 1879: 64, pl. 4 figs 6-7. – Kramp, 1955: 153, synonym.

Tiara conifera Haeckel, 1879: 59. – Kramp, 1955: 152, re-examination of type specimen, synonymy.

in part *Perigonimus vesicarius*. – Naumov, 1969: 202, ? not fig. 69.

Type locality: Nahant, Massachusetts Bay, USA.

Material examined: See Schuchert (2007). The molecular comparisons of this study included also 16S sequences of the material described in Prudkovsky & Neretina (2016), as well as of a medusa from the Nuuk-Fjord in Greenland (GenBank KT809324) collected 22 June 2010 and identified by Russell Hopcroft. It had about 28-30 tentacles, about as many rudimentary bulbs, and a large apical projection (after data and photos kindly provided by R. Hopcroft).

Diagnosis: *Catablema* medusa with bell up to 25 mm wide and 30 mm high, including the large, globular apical projection; gonads in long, irregular folds, oblique in lateral parts, almost perpendicular in middle part of each quadrant, with or without pits on gonad folds; 24-32 tentacles, rarely up to 48, often with small, rudimentary bulbs between two tentacle pairs; usually with small abaxial ocelli on at least some tentacles or bulbs, sometimes missing; mesenteries short.
Hydroid arising from reticulate stolons on bivalves, hydranths stolonal or with very short pedicel only, base of hydranth surrounded by a membranous pseudohydrotheca; hydranth fusiform, up to 0.75 mm long, conical hypostome, 3-8 filiform amphicoronate tentacles in a single whorl. Medusa buds arise from stolons, diameter reaches sizes similar as hydranths, young medusa released with two opposite tentacles only.

Description and illustrations: See Schuchert (2007) and Prudkovsky & Neretina (2015).

Distribution: An Arctic species, rarely penetrating into boreal regions.

Remarks: The medusae identified by Prudkovsky & Neretina (2016) had up to 28 tentacles, matched thus exactly the concept of *C. vesicarium* given in Kramp (1959) and also in the original description of Agassiz (1862, 1865). Likewise, the 16S and COI sequences of the sample from Greenland (GenBank KT809324) are derived from a typical specimen and can also be used as a reliably identified reference specimen and sequence.
Although *C. nodulosum* is likely conspecific with *C. vesicarium*, it is discussed separately below to allow a better separation and clearer presentation of this morphotype.

Catablema vesicarium nodulosum Bigelow, 1913
Fig. 11

Catablema vesicarium var. *nodulosa* Bigelow, 1913: 17, pl. 1 figs 8-9.

Catablema nodulosa. – Arai & Brinckmann-Voss, 1980: 45, fig. 21.

Type locality: Dutch Harbour, Unalaska Island, USA.

Material examined: 2 specimens, not in permanent collection; USA, San Juan Islands, Friday Harbor, 48.5451° -123.01206°; collection date 16.05.2011 and 20.05.2011; collected at water surface with a dipping jar; DNA isolates 932 and 957; GenBank numbers see Table 1.

Diagnosis: North Pacific *Catablema* medusa, up to 25 mm in size, including the apical projection of variable size and shape; gonads in long, irregular folds, oblique in lateral parts, almost perpendicular in middle part of each quadrant, gonadal folds usually without pits, rarely a few present; With 8 to 16 tentacles, rarely up to 25, with 2-6 small, rudimentary bulbs between adjoining tentacles, usually with small, inconspicuous abaxial ocelli on the rudimentary bulbs, fully formed tentacles lack ocelli; mesenteries about 1/3 of manubrium height. Manubrium gold-brown or peach colour in living specimens.
Hydroid unknown.

Description: See Arai & Brinckmann-Voss (1980).

Remarks: In the examined material, only the smaller tentacles and the rudiments had small ocelli, the fully developed tentacles lacked them.
Bigelow (1913) found that some *Catablema* medusae from the North Pacific differed in tentacle numbers and gonad structure from *C. vesicarium* he had seen in the North Atlantic. Although he states that they were probably still within the extremes of the nominal species and no morphological discontinuity existed, he treated them as

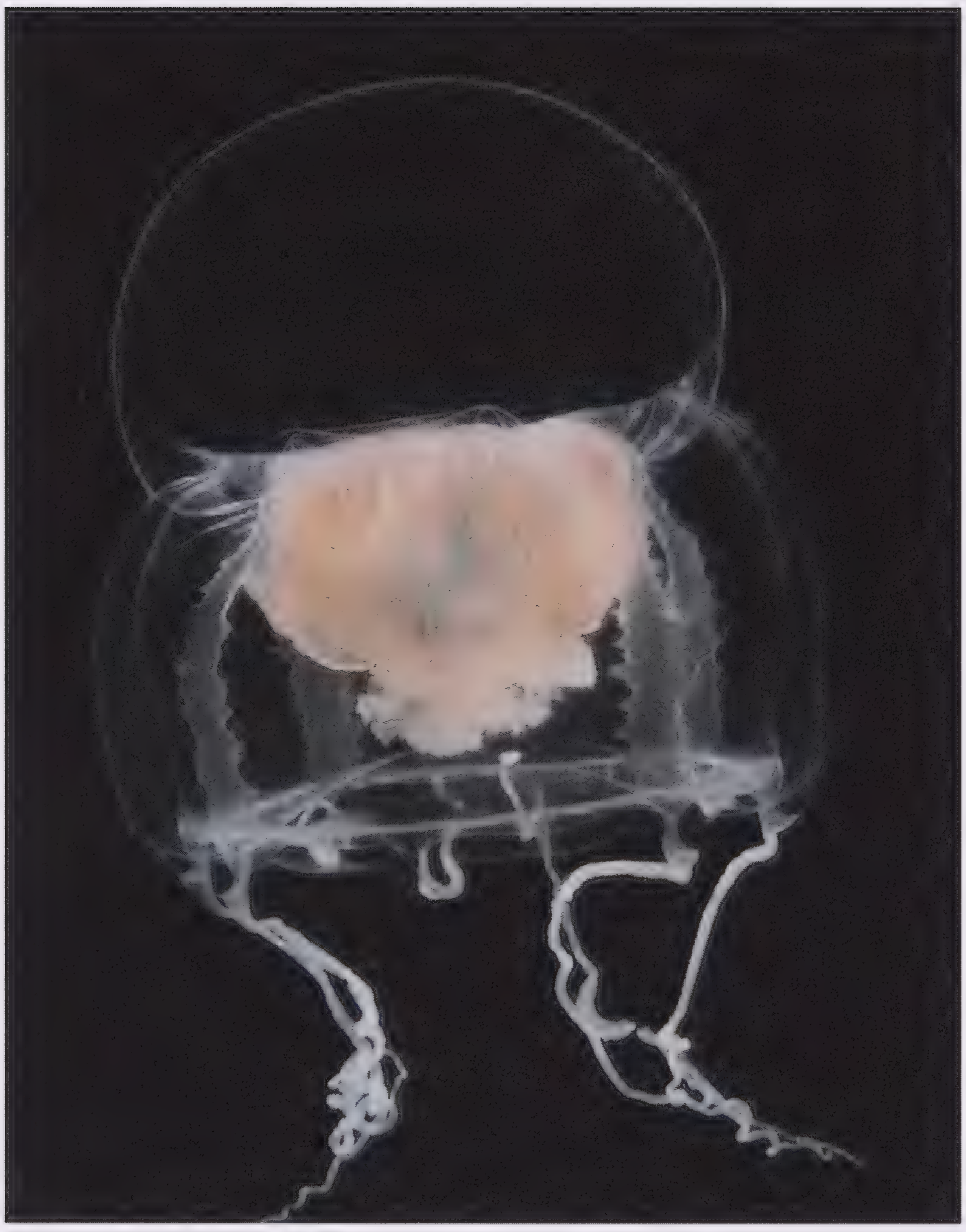

Fig. 11. *Catablema vesicarium nodulosum,* living medusa from Friday Harbor, WA, USA, bell height about 2 cm, the individual was used to obtain one of the DNA sequences of this study.

a variant of *C. vesicularium* and named it *Catablema vesicarium* var. *nodulosa.* Bigelow observed tentacle numbers of 14-25 tentacles, but the numbers were often difficult to establish as there was a continuum of sizes from mere knobs to fully grown tentacles. Hartlaub (1914: 321), Foerster (1924), and Kramp (1926, 1968) regarded *Catablema vesicarium* var. *nodulosa* Bigelow, 1913 as a synonym of *C. vesicarium*.

Arai & Brinckmann-Voss (1980) did not agree and raised the variant to full species level. They distinguished *Catablema nodulosum* from *C. vesicarium* solely on account of the lower tentacle number, being only 8-16 instead of 32. The shape of the gonads as argued by Bigelow (1913) was deemed unsuitable to distinguish the two species and I concur. Arai & Brinckmann-Voss (1980) based their decision on medusae from the southern limit of this genus, thus perhaps with a suboptimal growth. This could perhaps also explain the lower tentacle number compared to *C. vesicarium*, which is an Arctic species. Bigelow (1913), who had medusae from cooler waters (Aleutian Islands), founded his variety on animals having up to 25 tentacles. It is therefore reasonable to follow Bigelow, Hartlaub, and Kramp and regard *C. nodulosum* only gradually different from *C. vesicarium*, representing a local variant only. Moreover, tentacle numbers in Pandeidae medusae vary considerably and are deemed mostly unsuitable to delimit species. The COI sequence data did not show significant differences between the *nodulosa* form from the NE Pacific and typical *C. vesicarium* from the Greenland Sea (Fig. 9; the 16S data show very little divergences within this genus). *Catablema nodulosum* should therefore be regarded as conspecific with *C. vesicarium*, or at most be treated as a subspecies of the latter. According to the ICZN (§45.6.4), a name introduced as variety before 1961 gets the rank of subspecies.

Catablema multicirratum Kishinouye, 1910
Figs 12-13

Catablema multicirrata Kishinouye, 1910: 24.
Catablema multicirrata. – Bigelow, 1913: 19, pl. 1 figs 4-7. – Hartlaub, 1914: 321. – Kramp, 1926: 91, pl. 2.– Uchida, 1927: 213. – Uchida, 1933: 130 fig. 6. – Uchida, 1940: 286. – Uchida, 1969: 286. – Arai & Brinckmann-Voss, 1980: 44, fig. 20. – Wang *et al.*, 2014: 99, fig. 12.
Catablema multicirratum. – Kramp, 1961: 96. – Kramp, 1968: 50, fig. 133
Perigonimus multicirratus. – Naumov, 1969: 204, fig. 71.
Perigonimus breviconis. – Naumov, 1969: 204, fig. 72. [not *Neoturris breviconis* (Murbach & Shaerer, 1902)]

Type locality: Paramushir Island, Kuril Islands, Pacific Ocean.

Material examined: 1 specimen, not in permanent collection; USA, Friday Harbor Laboratories, floating docks, 48.54514° -123.01206°, 0.5 m depth; collection date 19.05.2011; depicted in Fig. 12; DNA isolate 868; GenBank numbers of sequences see Table 1. – Tissue samples and photos of two medusae here identified as *Catablema* cf. *multicirratum* from north of Svalbard obtained from Aino Hosia (University Museum of Bergen); the rest of the medusae in the collections of the Bergen Museum. The collection data are given in Table 1.

Diagnosis: *Catablema* medusa with umbrella height and diameter 30 to 65 mm including large dome-like apical projection corresponding to about half the total bell height. Manubrium with very broad, quadrangular base, long mesenteries, mouth margin variably folded, gonadal folds oblique to vertical, few or no pits. Mature animals with 80 to 160 tentacles, without or only few marginal bulbs between tentacles in adult specimens. Radial canals relatively short but very broad and with large, complex lateral outgrowths. No ocelli observed. Stomach and marginal bulbs light orange in living specimens.
Hydroid not known.

Remarks: *Catablema multicirratum* was somewhat inadequately described by Kishinouye (1910), with the sole diagnostic character distinguishing it from *C. vesicarium* being the tentacle number, given as "several hundreds." This must certainly be erroneous.

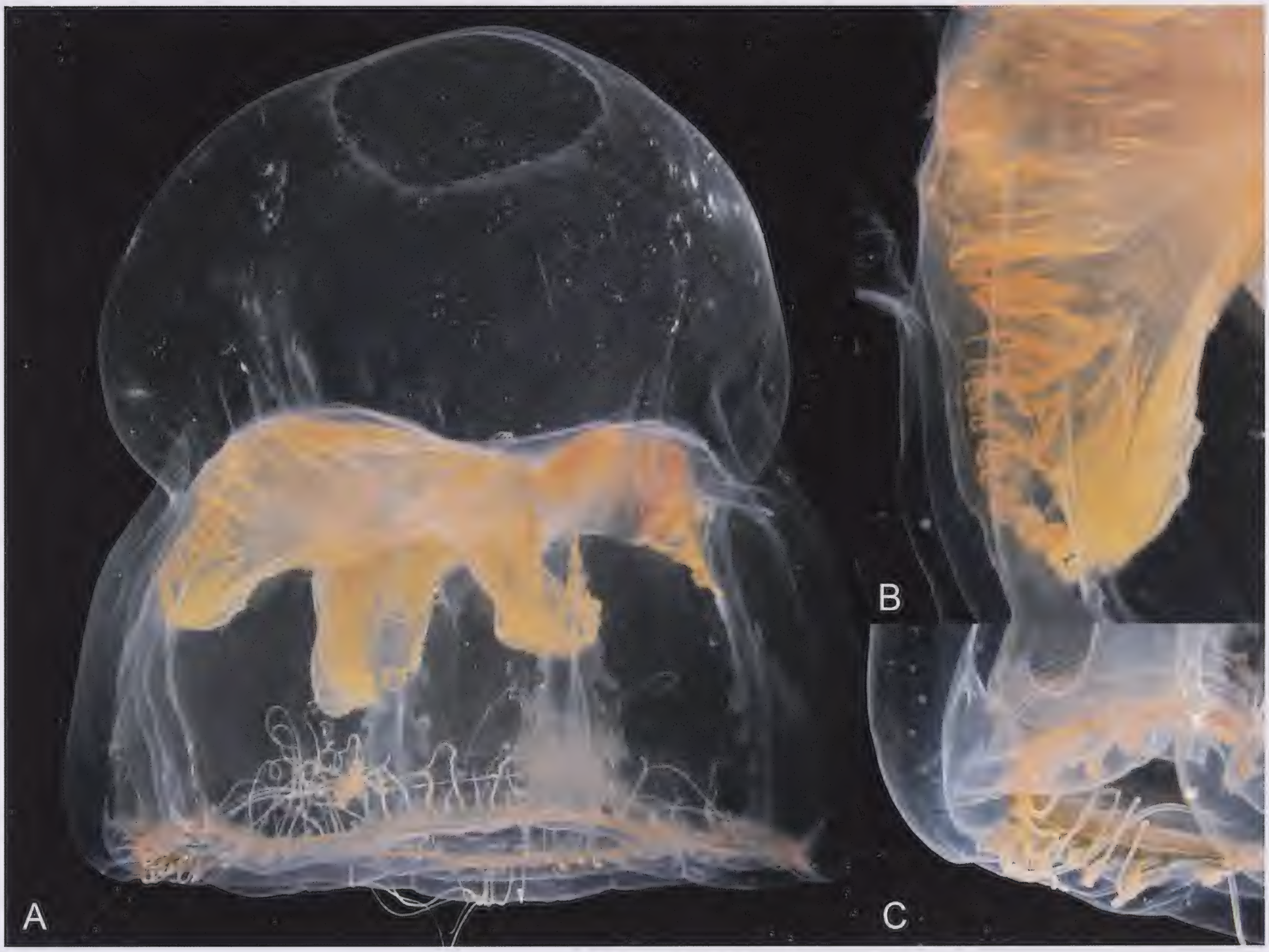

Fig. 12. *Catablema multicirratum*, living medusa from Friday Harbor, WA, USA, bell size about 6.5 cm, about 100 tentacles. The individual was used to obtain the DNA sequences of this study (DNA 868, see Table 1). (A) Whole medusa. The circular spot on the apical process is an area where the epidermis is lost due to contact with the water-air interface. (B) Detail of stomach with gonad folds. (C) Detail of umbrella margin with tentacles.

Bigelow (1913) then described and illustrated new material from the Bering Sea and the Gulf of Alaska. The species was subsequently also recorded from the west coast of Greenland by Kramp (1926). The Atlantic medusae were distinctly smaller, but had the same high number of tentacles. Although the species has been reported regularly (see Arai & Brinckmann-Voss, 1980; Wang *et al.*, 2014), only a few specimens have been documented. It seems that it has sometimes also been confused with *N. breviconis* (e.g. Naumov, 1969). According to our current knowledge the tentacle number permits a reliable separation of *C. vesicarium* and *C. multicirratum.*

The Pacific specimen of *Catablema multicirratum* used for this study was identified based on Arai & Brinckmann-Voss (1980). The single animal was very large, reaching 6.5 cm in height (Fig. 12) and had approximately 100 tentacles. It was thus easily separable from the *Catablema vesicarium nodulosum* (Fig. 11) found at the same place. The two medusae from Svalbard (Fig. 13) were smaller and had denser tissues with a darker orange colour than the Pacific specimen.

While morphologically separable, the status of the species remains somewhat problematic when using 16S, COI, and ITS sequence data. 16S and ITS sequences cannot be used to separate *C. multicirratum* from *C. vesicarium* (Fig. 8; Table 2). COI has about three times higher divergence values than 16S and permits to discern somewhat more structure in the *Catablema* clade (Fig. 9). The Pacific *Catablema multicirratum* separates from both, *C. vesicarium* and the Atlantic *C. multicirratum*. The Atlantic form is thus perhaps also an independent lineage and it was therefore named here *C.* cf. *multicirratum.*

The BOLD barcode database contains some additional COI sequences of *Catablema* samples, mostly identified as *C. vesicarium*. The origin of the material is from the Pacific and Atlantic coasts of Canada, but unfortunately the identifications are unreliable and the accompanying photos virtually useless. Due to the doubtful identities,

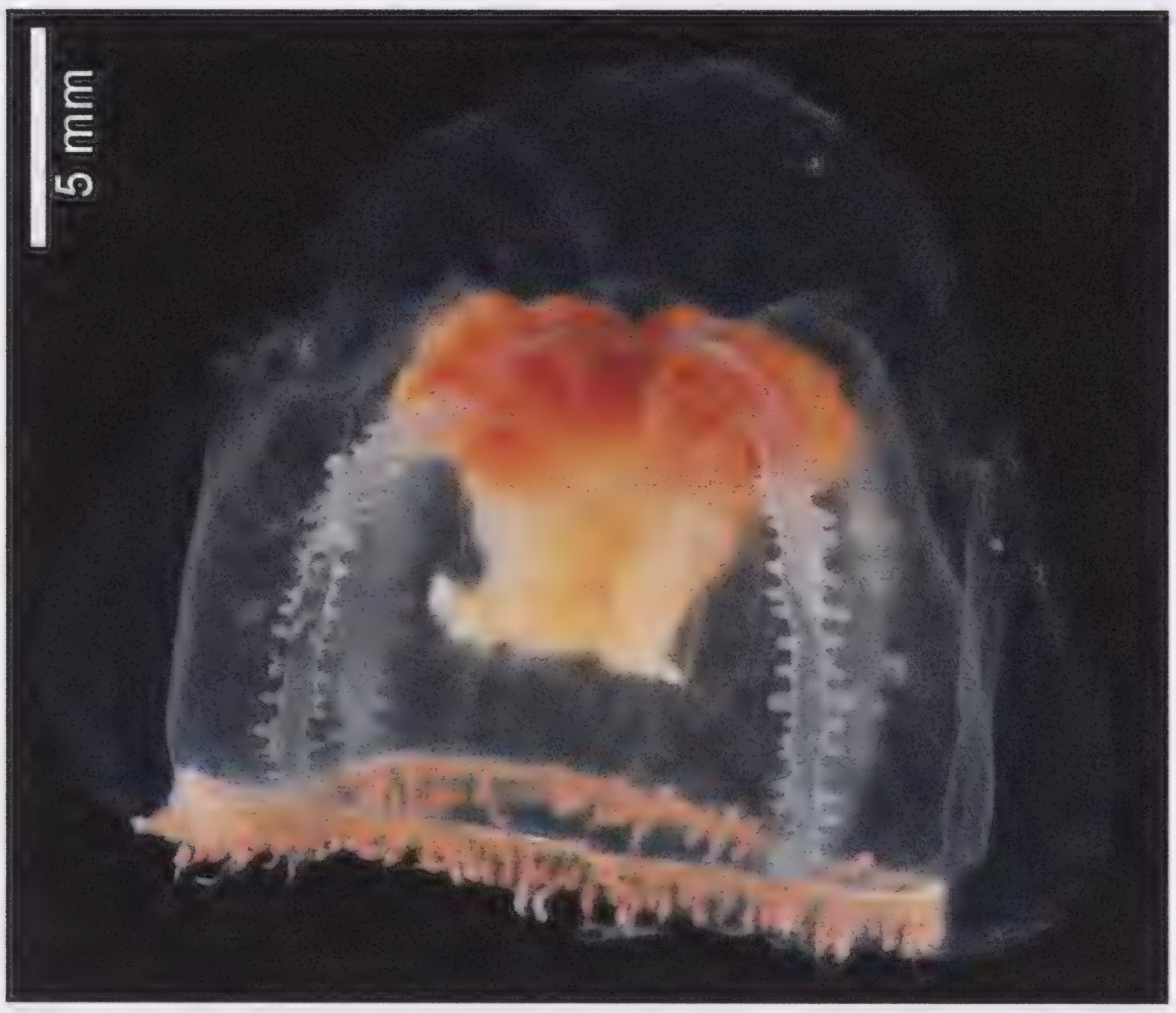

Fig. 13. *Catablema* cf. *multicirrata*, living subadult specimen from Svalbard (sample DNA 1139), photo courtesy of Aino Hosia. Note the high number of tentacles, estimated about 140 combined with the moderate size of the bell.

these sequences were therefore not included in the analyses of this study. Adding nevertheless these sequences to the ML-analysis (results not shown), the results remain similar to the one shown in Fig. 9. *Catablema* appears to be split into three clades with relatively low divergences: *C. vesicarium*, *C. multicirratum*, and *Catablema* from Svalbard.

However, it must be concluded that more *Catablema* samples with a thorough documentation and identification of the specimens are needed before any reliable conclusion is possible. Markers with more resolving power (e.g. microsatellites) might be necessary to settle the status of all nominal *Catablema* species. It is still possible that they all represent only different age groups and local variants.

Genus *Leuckartiara* Hartlaub, 1914

Type species: *Geryonia octona* Fleming, 1823 (Kramp, 1959).

Remarks: For the diagnosis see Bouillon *et al.* (2006) or Schuchert (2007). A key to all species is provided by Xu & Huang (2004), a comparative table of the species is also presented in Pagès *et al.* (1992). A list of all species, including also the ones described after 2004, is given in Schuchert (2017b).

Leuckartiara cf. *octonema* Xu, Huang & Guo, 2007

Leuckartiara octonema Xu, Huang & Guo, 2007: 70, fig. 5.

Type locality: Upwelling zone in the southern part of the Taiwan Strait (21°40’-23°51’N 116°47’-118°56’E).

Material examined: MHNG-INVE-97018; hydroid colony, young medusae, and medusae cultivated to maturity (31 days) by Takanori Suehiro; Japan, Mie, Honshu, Toba City, intertidal zone, 34.47806°N 136.8675°E; date collected 09.05.2014; DNA sample 1208; for GenBank number of sequences see Table 1.

Remarks: The material used to obtain the DNA sample and the details of the life cycle will be described by Suehiro & Kubota (2018).

The morphology of the adult medusa corresponds to *Leuckartiara octonema*, except for the presence of ocelli on the rudimentary bulbs. Therefore, the species was provisionally identified as *Leuckartiara* cf. *octonema* only, pending further sequence comparisons with specimens from near the type locality.

Leuckartiara longicalcar n. spec.
Figs 14, 15A-C, 16

in part *Leuckartiara octona*. – Mackie & Mackie, 1963: 68. [not *L. octona* (Fleming, 1823)]

Leuckartiara species. – Arai & Brinckmann-Voss, 1980: 56, fig. 30.

Holotype: MHNG-INVE-98638; female; USA, San Juan Island, Friday Harbor, 48.54514° -123.01206°,

Fig. 14. *Leuckartiara longicalcar*, n. spec., living animal (paratype), total height about 15 mm.

depth 0.5 m; collection date 20.05.2011; preserved in formalin, subsequently transferred to ethanol.

Paratypes: MHNG-INVE-78922, 9 specimens; USA, San Juan Island, Friday Harbor, 48.54514° -123.01206°, depth 0.5 m; collection date 20.05.2011; one specimen used to isolate DNA 869; for GenBank numbers of sequences see Table 1. – MHNG-INVE-82312, 2 specimens; Canada, British Columbia, Salish Sea, 49.2505° -123.74867°, depth 0-50 m; collected by Moria Galbraith; preserved in formalin, subsequently transferred to ethanol.

Additional data: Several photographs of living medusae taken by Kevin Lee off the coast of Palos Verdes, California, USA, 33.8211° -118.4569°, one of the photos is reproduced here in Fig. 16.

Etymology: From the Latin *longus*, long, and *calcar*, spur, referring to the long abaxial spurs of the tentacle bulbs.

Type locality: USA, San Juan Island, Friday Harbor, 48.54514°N 123.01206°W.

Diagnosis: *Leuckartiara* medusa 15-20 mm total height, with large pointed apical process of about 1/3 to 2/5 of total bell height, umbrella higher than wide; up to 16-24 tentacles, between each tentacle pair 1-3 small, rudimentary bulbs, perradial and interradial tentacles with conspicuous, long, pointed abaxial spurs

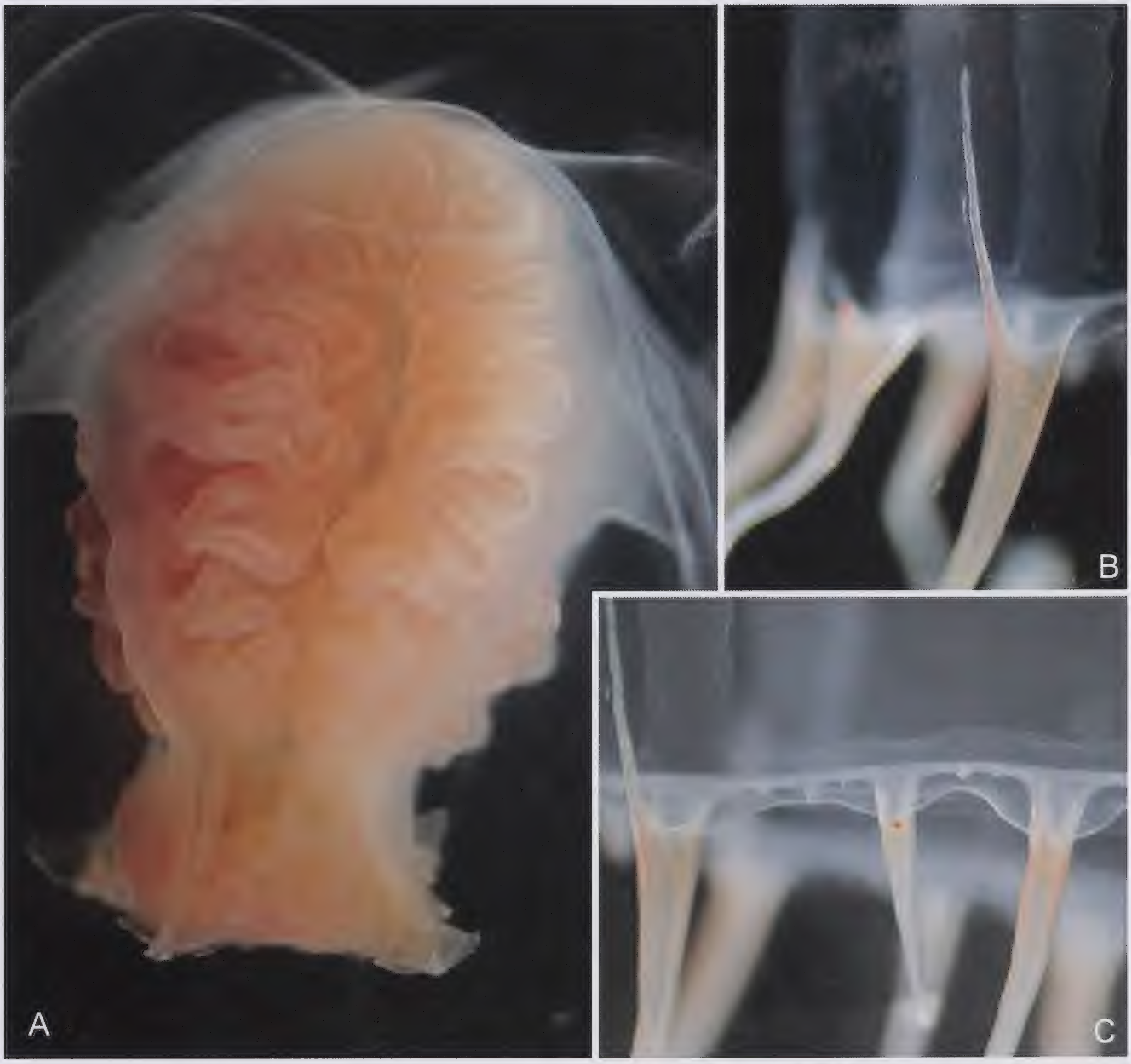

Fig. 15. *Leuckartiara longicalcar*, n. spec., living animal. (A) Details of manubrium with gonad folds. (B) Lateral view of a perradial tentacle with the characteristic, long, abaxial spur. (C) Adradial tentacles and rudimentary bulbs, note red ocelli.

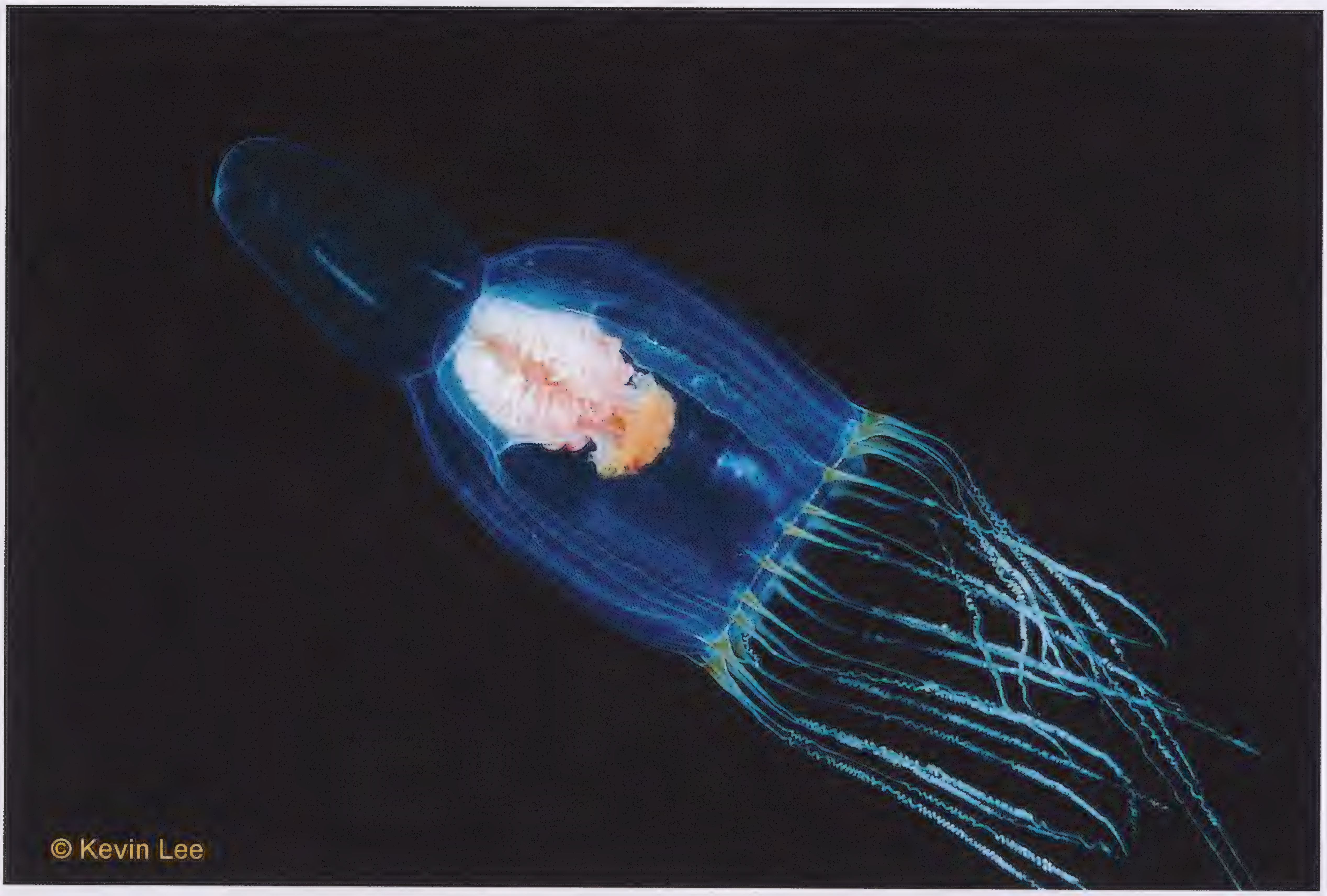

Fig. 16. *Leuckartiara longicalcar*, n. spec., living animal, height 13-18 mm, photographed by Kevin Lee off Los Angeles, California, USA. Note, this photograph is copyright protected and permission to use it here has been obtained by paying a royalty fee to the author and copyright holder Kevin Lee (www.diverkevin.com).

reaching up to 1/6 of the bell height; tentacles and bulbs lacking tentacles usually with small red abaxial ocelli. Manubrium about 1/2 of subumbrellar height, pale-orange, with long mesenteries, mouth cruciform, mouth margin moderately ruffled. Gonads in adradial series of horizontal folds, distinct interradial connecting fold absent.

Description: *Leuckartiara* medusa up to 15-20 mm in height and about 10 mm in diameter when mature, with a large, pointed apical process of about 1/3 to 2/5 of total bell height, umbrella higher than wide. Interradial, subumbrellar pockets of variable size present.
Manubrium about half the height of the subumbrellar height, shaped like inverted vase, connected to radial canals via long mesenteries (about 1/3 of manubrium height). Manubrium base and mouth opening cruciform, mouth rim moderately ruffled.
Gonad tissue in 8 series of broad, adradial, horizontal folds, 8-12 folds in an adradial series, many folds with a central depression and resembling a loop or simply bifurcated (Fig. 15A). The two series of gonad folds of one quadrant usually not connected by a fold across the interradial region as in other congeners (thus without the H-form of the gonad folds, often described as "horse-shoe shape" in older publications, comp. Fig. 17C). Sometimes an inconspicuous interradial connection of the two rows of folds may be present at the aboral end of the manubrium. No gonadal pits. Egg size about 0.1 mm. Radial canals slightly jagged and broad. Ring canal smooth, broad.
Tentacles usually 16, sometimes up to 24, between each tentacle pair 1-3 small, rudimentary bulbs without tentacles. Bases of tentacles laterally compressed, clasping bell margin. Perradial and interradial tentacle bases (oldest tentacles) with long, pointed abaxial spurs, reaching up to 1/6 of the bell height (Fig. 15B), shorter (younger) tentacles with short spur or no spur. Spurs appear solid, without internal canal. A small red ocellus present on most tentacles and also rudimentary bulbs, situated on abaxial side at interface of tentacle to exumbrella, in tentacles with long abaxial spurs ocelli at end of spur.
Colour: Manubrium pale orange, proximal parts of tentacles pale orange to yellowish, ocelli orange-red.
Nematocysts of tentacles microbasic heteronemes, ca. 4 x 7 μm.

Distribution: North-eastern Pacific, from Vancouver Island to Southern California.

Remarks: This species was described by Arai & Brinckmann-Voss (1980: 56) as *Leuckartiara* species distinct from *L. octona*. Dr Anita Brinckmann-Voss (pers. com., 2013) told me that she initially intended to name it in a subsequent publication, but was now unable to do it and encouraged me to do it myself.

Leuckartiara longicalcar does not match any of the known species (Kramp, 1968; Pages *et al.*, 1992; Xu & Huang, 2004; Schuchert, 2017). It has previously been misidentified as *L. octona* (Fleming, 1823) and been considered related to *L. zacae* Bigelow, 1940 (see Arai & Brinckmann-Voss, 1980).

Leuckartiara octona is indeed similar in appearance, but lacks the long abaxial spurs and regularly has a fold across the interradial region connecting the adradial series of folds. The 16S and COI sequence data (Figs 8-9) clearly separated *L. longicalcar* from the Atlantic *L. octona*, although they are closely related.

Leuckartiara zacae Bigelow, 1940 is a rare species first found in the Gulf of Panama. It is somewhat larger than *L. longicalcar* and has about the same number of tentacles. The most prominent difference is the length of the tentacle spurs: they are much longer and extend up to 2/3 of the bell height. Bigelow (1940) described them as exumbrellar ribs containing a thin gastrodermal canal. Additionally, *L. zacae* has no apical process (but Kramp (1965) observed a small process in a juvenile specimen from Indonesia, the identity of this material is perhaps questionable), the umbrella without the process is larger (21 versus 12 mm), the manubrium is more voluminous and has more gonadal folds. It is only known to occur in tropical seas (Kramp, 1965).

Other *Leuckartiara* species with tentacle spurs are *L. gardineri* Browne, 1916, *L. acuta* Brinckmann-Voss, Arai & Nagasawa, 2005, and *L. fujianensis* Huang, Xu, Lin & Qiu, 2008. All three have only four fully formed tentacles.

Kevin Lee (2017) published a series of magnificent photos of *Leuckartiara* medusae observed off Los Angeles, California. One of them is reproduced here (Fig. 17). These medusae must clearly be referred to *L. longicalcar* n. spec. Some of the individuals are almost identical to the ones shown here, while others (Fig. 17) appear somewhat larger, with up to 24 tentacles, and a more voluminous stomach. Some of the individuals have a more intense colour, appearing more reddish, and also the tentacle bases show some reddish pigments. The distribution of the species extends thus from Vancouver Island to Southern California.

Leuckartiara spec.
Fig. 17A-C

Material examined: MHNG-INVE-78921, 1 of originally 2 specimens; USA, San Juan Island, Friday Harbor, 48.54514° -123.01206°, depth 0.5 m; collection date 22.05.2011; one medusa used to extract DNA,

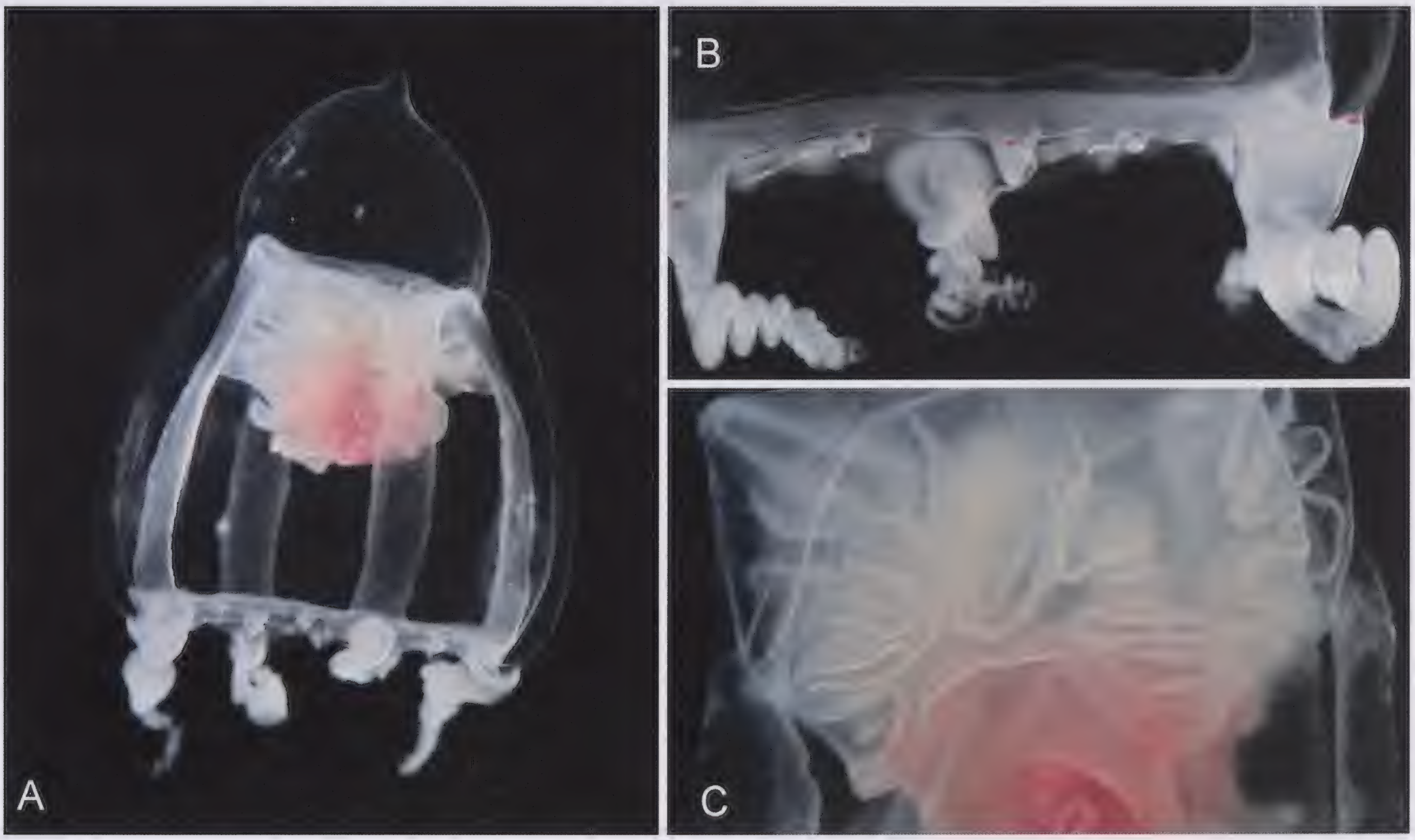

Fig. 17. *Leuckartiara* spec., living animal. (A) Whole medusa. (B) Bell margin with tentacle bases. (C) Details of manubrium with gonad folds (immature?).

isolate 871; for GenBank numbers of sequences see Table 1.

Diagnosis: Subadult *Leuckartiara* medusa up to 8 mm total height, with large pointed apical process of about 1/3 of total bell height, umbrella as wide as high. 4 perradial tentacles, 4 shorter interradial tentacles, 8 adradial small stumps or thin- and short tentacles. Tentacle bases not much laterally compressed, not clasping bell margin, without abaxial spurs, with red abaxial ocelli. Manubrium base and mouth cruciform, mouth margin with some folds. Gonad folds on manubrium in typical H-like arrangement, adradial folds directed perradially. Radial canals very broad, smooth, long mesenteries present (about 1/2 of manubrium height).

Remarks: These two medusae were obviously not fully developed and they could not positively be identified with any species described in Arai & Brinckmann-Voss (1980). Most probably it belongs to the species identified as *L. nobilis* Hartlaub, 1914 by Foerster (1924) and Arai & Brinckmann-Voss (1980). The latter authors report that their adults reached 22 mm in height. The younger specimens described by Foerster (1924) agreed with the current material. The 16S and COI sequences, however, did not match the Atlantic specimen of *L. nobilis*. The latter was described in Schuchert (2007), but it was also not fully mature. More Atlantic and Pacific specimens fitting the description of this rare species must be examined in order to get a clearer picture of its identity.

Genus *Halitholus* Hartlaub, 1914

Type species: *Halitholus pauper* Hartlaub, 1914 (Kramp, 1959).

Remarks: For the diagnosis see Bouillon *et al.* (2006) or Schuchert (2007).

Halitholus spec.

Fig. 18A-C

in part *Leuckartiara octona*. – Mackie & Mackie, 1963: 68 [not *L. octona* (Fleming, 1823)]

Halitholus species I. – Arai & Brinckmann-Voss, 1980: 48, figs 23-24.

Material examined: 1 female specimens, not in permanent collection; USA, San Juan Island, Friday

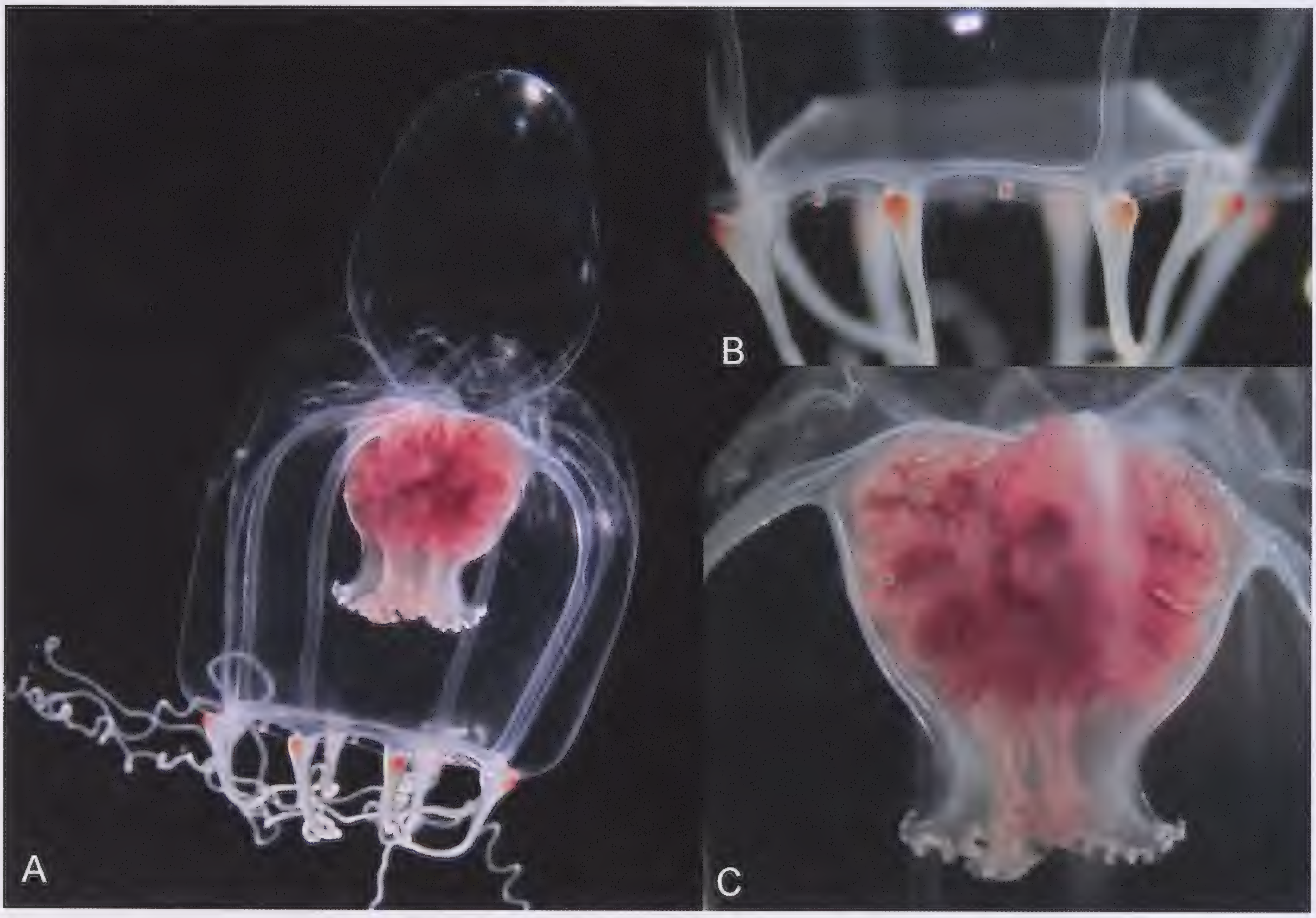

Fig. 18. *Halitholus* spec., living animal. (A) Whole medusa. (B) Bell margin with tentacle bases. (C) Details of manubrium with gonad folds. Note the clearly visible oocytes.

Harbor, 48.54514° -123.01206°, depth 0.5 m; collection date 20.05.2011; DNA isolate 870; for GenBank numbers of sequences see Table 1.

Remarks: This species was described by Arai & Brinckmann-Voss (1980) as *Halitholus* species I. They kept it distinct from *H. pauper* Hartlaub, 1914 on account of the lacking interradial gonad-fold connection and the smoother radial canals. However, the latter character appears not so convincing. As they also found a second similar morphotype (as *Halitholus* species II) they did not describe it as a new species.

I suspect that *Halitholus* species I and *Halitholus pauper* in Arai & Brinckmann-Voss (1980) are the same, but it is not clear if they are really conspecific with *H. pauper* from the Atlantic Ocean (see Schuchert, 2007 for description). In Atlantic *H. pauper*, the interradial tentacles are usually not fully developed and the deep interradial subumbrellar pockets as visible in Fig. 18A have not been reported. Good photographs and also DNA barcode sequences of the Atlantic form are needed to evaluate more precisely the specific identity of the present material.

Even though the present medusa had no distinct mesenteries (Fig. 18A), the only character that distinguishes the genus *Halitholus* from *Leuckartiara*, the 16S and COI sequences placed it close to *Leuckartiara octona*, type species of the genus (Figs 8-9). The other *Halitholus* species used in the analysis, *H. cirratus*, did not cluster with the *Halitholus* from Friday Harbor, which casts some doubts on the validity of the genus.

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REFERENCES

Agassiz L. 1862. Contributions to the natural history of the United States of America. Vol. IV. *Little Brown, Boston*, pp. 1-380, pls 1-19.

Agassiz A. 1865. North American Acalephae. *Illustrated Catalogue of the Museum of Comparative Zoölogy at Harvard College* 2: 1-234.

Agassiz A., Mayer A.G. 1902. Medusae. Report of the scientific research expedition to the tropical Pacific. U.S. Fish Comm. St. Albatross, 1899-1900. III. *Memoirs of the Museum of Comparative Zoology at Harvard College* 26(3): 136-176, pls 1-14.

Arai M.N., Brinckmann-Voss A. 1980. Hydromedusae of British Columbia and Puget Sound. *Canadian Bulletin of Fisheries and Aquatic Sciences* 204: 1-192.

Bavestrello G. 1985. Idroidi simbionti di paguri e gasteropodi nella riviera Ligure di Levante. *Oebalia* 11(1): 349-362.

Bigelow H.B. 1909a. The Medusae. Reports on the scientific results of the expedition to the eastern tropical pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer "Albatross" from October, 1904, to March, 1905. XVI. *Memoirs of the Museum of comparative Zoology at Harvard College* 37: 1-243, plates 1-48.

Bigelow H.B. 1909b. Coelenterates from Labrador and Newfoundland, collected by Mr. Owen Bryant from July to October, 1908. *Proceedings of the United States National Museum* 37(1706): 301-320, pls 30-32.

Bigelow H.B. 1913. Medusae and Siphonophora collected by the U.S. steamer "Albatross" in the Northwestern Pacific. *Proceedings of the United States National Museum* 44(1946): 1-119, pls 1-6.

Bigelow H.B. 1940. Eastern Pacific Expeditions of the New York Zoological Society. XX. Medusae of the Templeton Crocker and Eastern Pacific Zaca Expeditions, 1936-1938. *Zoologica, N.Y.* 25(3): 281-321.

Bouillon J., Gravili C., Pagès F., Gili J.M., Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Museum National d'Histoire Naturelle* 194: 1-591.

Brinckmann-Voss A., Arai M.N., Nagasawa K. 2005. *Leuckartiara acuta* (Hydrozoa, Anthoathecatae, Pandeidae), a new species from the Pacific. *Publications of the Seto Marine Biological Laboratory* 40(3-4): 131-139.

Browne E.T 1916. Medusae from the Indian Ocean. *Transactions of the Linnean Society of London, Zoology* 17(2): 169-209.

de Blainville H.M.D. 1830. Dictionnaire des Sciences naturelles. *F.G. Levrault, Paris*, pp. 1-548.

Edwards C. 1965. The hydroid and the medusa *Neoturris pileata*. *Journal of the Marine Biological Association of the United Kingdom* 45(2): 443-468.

Fabricius O. 1780. Fauna Groenlandica. *G. Rothe, Hafniae and Lipsiae,* 452 pp., 1 plate. https://doi.org/10.5962/bhl.title.13489

Fleming J. 1823. Gleamings of natural history, gathered on the coast of Scotland during a voyage in 1821. *Edinburgh Philosophical Journal* 8: 294-303.

Foerster R.E. 1924. The Hydromedusae of the west coast of North America, with special reference to those of the Vancouver Island Region. *Contribution to Canadian Biology*, (new ser.) 1(12): 219-277.

Folmer O., Black M., Hoeh W., Lutz R., Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294-9.

Forbes E. 1846. On the Pulmograde Medusae of the British Seas. *Annals and Magazine of Natural History* (ser. 1) 18: 284-287.

Forbes E. 1848. A monograph of the British naked-eyed medusae: with figures of all the species. *Ray Society, London,* 104 pp., 13 pls. https://dx.doi.org/10.5962/bhl.title.10032

Forsskål P. *In:* Niebuhr C.E. 1775. Descriptiones animalium avium, amphibiorium, piscium, insectorum, vermium; quae

in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr. *Mölleri, København*, pp. 1-164. https://dx.doi.org/10.5962/bhl.title.2154

Forsskål P. *In:* Niebuhr C.E. 1776. Icones rerum naturalium, quas in itinere orientali depingi curavit Petrus Forskål, Prof. Haun. Post mortem auctoris ad Regis mandatum æri incisas edidit Carsten Niebuhr. Copenhagen: Mölleri, 15 pp., 43 pls. https://dx.doi.org/10.5962/bhl.title.70772

Goy J. 1995. Les méduses de François Péron et Charles-Alexandre Lesueur. Un autre regard sur l'expédition Baudin. *Ministère de l'enseignement supérieur et de la recherche. Comité des travaux historiques et scientifiques, Paris*, 392 pp.

Haeckel E. 1879. Das System der Medusen. Erster Teil einer Monographie der Medusen. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 1: XX+1-360, 20 plates. https://dx.doi.org/10.5962/bhl.title.46856

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.

Hartlaub C. 1892. Zur Kenntniss der Anthomedusen. *Nachrichten von der Gesellschaft der Wissenschaften zu Göttingen, Mathematisch-Physikalische Klasse*: 17-22.

Hartlaub C. 1914. Craspedote Medusen. Teil 1, Lieferung 3, Tiaridae. *Nordisches Plankton* 6: 237-363.

Hosia A., Båmstedt U. 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Marine Ecology Progress Series* 351: 113-127.

Huang J.Q., Xu Z.Z., Lin J.Z., Qiu M.F. 2008. Three new species of Anthomedusae (Hydrozoa, Hydroidomedusae) from the Fujian sea water. *Journal of Xiamen University Natural Science* 47(3): 408-412.

Kishinouye K. 1910. Some Medusae of Japanese waters. *Journal of the College of Science, Imperial University of Tokyo* 27(9): 1-35, pls 1-5.

Kramp P.L. 1926. Medusae. Part II. Anthomedusae. *Danish Ingolf Expedition* 5(10): 1-102, pls 1-2.

Kramp P.L. 1955. A revision of Ernst Haeckel's determinations of a collection of Medusae belonging to the Zoological Museum of Copenhagen. *Deep Sea Research* 3: 149-168.

Kramp P.L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1-283.

Kramp P.L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom* 40: 1-469.

Kramp P.L. 1965. The hydromedusae of the Pacific and Indian Oceans. *Dana Report* 63: 1-162.

Kramp P.L. 1968. The hydromedusae of the Pacific and Indian Oceans. Sections II and III. *Dana Report* 72: 1-200.

Kramp P.L., Damas D. 1925. Les méduses de la Norvège. Introduction et partie spéciale. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 80: 217-323.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A., McWilliam H., Valentin F., Wallace I.M., Wilm A., Lopez R., Thompson J.D., Gibson T.J., Higgins D.G. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947-2948. http://dx.doi.org/10.1093/bioinformatics/btm404

Le Danois E. 1914. Coelentérés du plankton recueillis pendant la croisière du yacht «Pourquoi-Pas» dans l'Atlantique Nord et l'Océan Glacial (sous le commendement du Dr. Charcot). *Bulletin de la Société zoologique de France* 38: 13-34.

Lee K. 2017. *Leuckartiara* spp. (?) Blue water dive, miles offshore Palos Verdes, California USA. Available at: http://www.diverkevin.com/keyword/Leuckartiara/i-JbD-Brff/X2 [Accessed 26.09.2017].

Lesson R.P. 1843. Histoire naturelle des zoophytes. Acalèphes. *Librairie Encyclopédique de Roret, Paris*, 596 pp.

Leuckart R. 1856. Beiträge zur Kenntniss der Medusenfauna von Nizza. *Archiv für Naturgeschichte* 22(1): 1-40, pls 1-2.

Lindsay D.J., Grossmann M.M., Nishikawa J.U.N. 2015. DNA barcoding of pelagic cnidarians: current status and future prospects. *Bulletin of the Plankton Society of Japan* 62(1): 39-43.

Mackie G.O., Mackie G.V. 1963. Systematic and biological notes on living hydromedusae from Puget Sound. *Bulletin (National Museum of Canada). Biological series* 199: 63-84.

Mayer A.G. 1910. Medusae of the world. Hydromedusae, Vols. I & II. Scyphomedusae, Vol III. *Carnegie Institution, Washington*, 735 pp., pls 1-76.

Murbach L., Shaerer C. 1902. Preliminary report on a collection of medusae from the coast of British Columbia and Alaska. *Annals and Magazine of Natural History* (7)9: 71-73.

Murbach L., Shearer C. 1903. On medusae from the coast of British Columbia and Alaska. *Proceedings of the Zoological Society of London* 2: 164-192, pls 17-22.

Naumov D.V. 1960. Gidroidi i gidromeduzy morskikh, solonovatovodnykh i presnovodnykh basseinov SSSR. *Opredeleteli po faune SSSR, Izdavaemye Zoologicheskim Institutom Akademii Nauk SSSR* 70: 1-626.

Naumov D.V. 1969. Hydroids and Hydromedusae of the USSR. *Israel Program for scientific translation*, 463 pp., 30 pls.

Oken L. 1815. Okens Lehrbuch der Naturgeschichte. Dritter Theil. Zoologie. *Reclam, Jena*, XXVIII, 850, XVIII pp.

Pagès F., Gili J.M., Bouillon J. 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina* 56 (Suppl. 1): 1-64.

Patterson R. 1859. On a new naked-eyed medusa. *Proceedings of the Dublin University Zoological and Botanical Association* 1(3): 279-281.

Péron F., Lesueur C.A. 1810. Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. *Annales du Muséum national d'histoire naturelle de Paris* 14: 325-366.

Prudkovsky A.A., Neretina T.V. 2016. The life cycle of *Catablema vesicarium* (A. Agassiz, 1862) (Hydrozoa, Pandeidae). *Polar Biology* 39(3): 533-542. https://dx.doi.org/10.1007/s00300-015-1805-x

Rees W.J. 1938. Observations on British and Norwegian hydroids and their medusae. *Journal of the Marine Biological Association of the U. K.* 23: 1-42.

Rees W.J. 1956. A revision of some northern gymnoblastic hydroids in the Zoological Museum, Oslo. *Nytt Magasin for Zoologi* 4: 109-120.

Rees W.J., Russell F.S. 1937. On rearing the hydroids of certain medusae, with an account of the methods used. *Journal of the Marine Biological Association of the United Kingdom* 22: 61-82.

Rothlisberg P.C., Pearcy W.G. 1976. An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fishery Bulletin* 74: 994-997.

Russell F.S. 1953. The medusae of the British Isles. *Cambridge University Press*, *London*, 530 pp., 35 pls.

Russell F.S. 1970. The Medusae of the British Isles. II Pelagic Scyphozoa with supplement to the first volume on Hydromedusae. *Cambridge University Press*, *Cambridge*, 284 pp.

Sars M. 1835. Beskrivelser og jagttagelser over nogle mærkelige eller nye i havet ved den Bergenske kyst levende dyr af polypernes, acalephernes, radiaternes, annelidernes og molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne ar. *T. Hallager*, *Bergen*, xii+81 pp. https://dx.doi.org/10.5962/bhl.title.13017

Sars G.O. 1874. Bidrag til Kundskaben om Norges Hydroider. *Forhandlinger i Videnskabs-Selskabet i Kristiana* 1873: 91-150, pls 2-5.

Schuchert P. 2005. Species boundaries in the hydrozoan genus *Coryne*. *Molecular Phylogenetics and Evolution* 36: 194-199. https://dx.doi.org/10.1016/j.ympev.2005.03.021

Schuchert P. 2007. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 2. *Revue suisse de Zoologie* 114(2): 195-396.

Schuchert P. 2012. North-West European Athecate Hydroids and their Medusae. Synopses of the British Fauna (New Series) 59. *The Linnean Society of London*, *London*, viii, 364 pp.

Schuchert P. 2014. High genetic diversity in the hydroid *Plumularia setacea*: A multitude of cryptic species or extensive population subdivision? *Molecular Phylogenetics and Evolution* 76: 1-9. https://dx.doi.org/10.1016/j.ympev.2014.02.020

Schuchert P. 2016. The polyps of *Oceania armata* identified by DNA barcoding (Cnidaria, Hydrozoa). *Zootaxa* 4175(6): 539-555. https://dx.doi.org/10.11646/zootaxa.4175.6.3

Schuchert P. 2017a. Pandeidae Haeckel, 1879. *In:* Schuchert P. (2017). World Hydrozoa Database. Accessed at http://www.marinespecies.org/hydrozoa/aphia.php?p=taxdetails&id=15029 on 2017-12-12

Schuchert P. 2017b. *Leuckartiara* Hartlaub, 1914. *In:* Schuchert P. (2017). World Hydrozoa database. Accessed at http://www.marinespecies.org/hydrozoa/aphia.php?p=taxdetails&id=117183 on 2017-09-18

Schuchert P., Hosia A., Leclère L. 2017. Identification of the polyp stage of three leptomedusa species using DNA barcoding. *Revue suisse de Zoologie* 124(1): 167-182. https://dx.doi.org/10.5281/zenodo.322675

Suehiro T., Kubota S. 2018. Life Cycle of *Leuckartiara* cf. *octonema*. *Kuroshio Biosphere* (submitted).

Uchida T. 1927. Studies on Japanese hydromedusae. I. Anthomedusae. *Journal of the Faculty of Science, Imperial University of Tokyo, Section IV, Zoology* 1(3): 145-241, plates 10-11.

Uchida T. 1933. Medusae from the vicinity of Kamchatka. *Journal of the Faculty of Science, Imperial University of Tokyo* 2(3): 125-133.

Uchida T. 1940. The Fauna of Akkesi Bay. XI. Medusae. *Journal of the Faculty of Science, Hokkaido Imperial University Series VI. Zoology* 7(3): 277-297.

Uchida T. 1969. Medusae from the Arctic Ocean. *Publication from the Seto marine biological Laboratoy* 17(4): 285-287.

Wang C., Huang J., Xiang P., Wang Y., Xu Z., Guo D., Lin M. 2014. Hydromedusae from the Arctic in 2010 during the 4th Chinese National Arctic Research Expedition (CHINARE 4). *Acta Oceanologica Sinica* 33(6): 95-102. https://dx.doi.org/10.1007/s13131-014-0494-6

Xu Z.-Z., Huang J.-Q. 2004. A survey on Anthomedusae (Hydrozoa: Hydroidomedusae) from the Taiwan Strait with description of new species and new combinations. *Acta Oceanologica Sinica* 23(3): 549-562.

Xu Z.-Z., Huang J.-Q., Guo D. 2007. A survey on Hydroidomedusae from the upwelling region of southern part of the Taiwan Strait of China. I. On new species and records of Anthomedusae. *Acta Oceanologica Sinica* 26(5): 66-75.

Zheng L., He J., Lin Y., Cao W., Zhang W. 2014. 16S rRNA is a better choice than COI for DNA barcoding hydrozoans in the coastal waters of China. *Acta Oceanologica Sinica* 33(4): 55-76. https://dx.doi.org/10.1007/s13131-014-0415-8

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Two new species of *Prototheora* Meyrick from the Democratic Republic of the Congo and Tanzania representing the northernmost records for the genus (Lepidoptera: Hepialidae)

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Abstract: The new species *Prototheora katangensis* Landry & Davis and *P. tanzaniensis* Davis & Landry are respectively described from the Haut-Katanga region of the Democratic Republic of the Congo and from the Makete District of Tanzania. The collecting localities are the northernmost known thus far for the genus *Prototheora* Meyrick.

Keywords: Prototheoridae - Ethiopian Region - Angola - Malawi - Republic of South Africa - Zimbabwe.

INTRODUCTION

Prototheora Meyrick was regarded in the past as the only genus of the family Prototheoridae Meyrick, but this family name has been synonymized with Hepialidae by Regier *et al*. (2015), a decision that is supported by the latest publication on the phylogeny of Hepialoidea (Simonsen & Kristensen, 2017). Prior to the present study, the genus included 13 species from the Ethiopian Region distributed mostly in the Republic of South Africa, but also Malawi (1 species), Angola (1 species), and Zimbabwe (1 species) (Davis, 1996, 2001, 2004; Mey, 2017). Thus, with the addition of the two species described herein the known fauna of *Prototheora* now stands at 15.

MATERIAL AND METHODS

The specimens reported here are deposited in the "Muséum d'histoire naturelle," Geneva, Switzerland (MHNG) and the Natural History Museum, University of Oslo, Norway (NHMO). The abdomens were detached, macerated, cleaned by BL at the MHNG, and sent in glycerin to DRD at the Natural History Museum, Smithsonian Institution, Washington, D.C., U.S.A. (NMNH) for description, drawing, and slide mounting. The photo of the holotype of *P. katangensis* (Fig. 1) and those of the head and genitalia in situ (Figs 2-5, 7-10) of both species were taken in the MHNG with a Leica DFC425 camera mounted on a Leica M205C stereoscopic microscope and the images were stacked using Zerene Stacker 1.04. The photo of the holotype of *P. tanzaniensis* (Fig. 6) was taken in the MHNG also with a Nikon D800 camera with a Micro-Nikkor 60 mm lens. The data recorded in the Material examined sections are transcribed exactly as found on the holotype labels, with vertical bars (|) to show changes of lines.

DESCRIPTIONS

Prototheora katangensis Landry & Davis sp. nov

Figs 1-5, 11, 13

Material examined

Holotype: ♂, 1- "H[au]t Katanga | Tshinkolobwe | 10.11.30 | J[ean]. Romieux" (on card stock in black ink with first and last lines printed); 2- "MHNG | ENTO | 00011170" (printed on white card stock in black ink); 3- "HOLOTYPE | Prototheora | katangensis | Landry & Davis" (hand-written on red card stock in black ink) (MHNG).

The MHNG number corresponds both to the database number and the genitalia slide number.

Type locality: Democratic Republic of the Congo, Haut-Katanga, Shinkolobwe.

Diagnosis: Similar in forewing pattern (Fig. 1) and size to several other species of *Prototheora*, this species can be separated from its congeners by the presence in the male genitalia (Figs 3-5, 11) of a distinct uncus and the shape of the tergal processes and valvae, notably.

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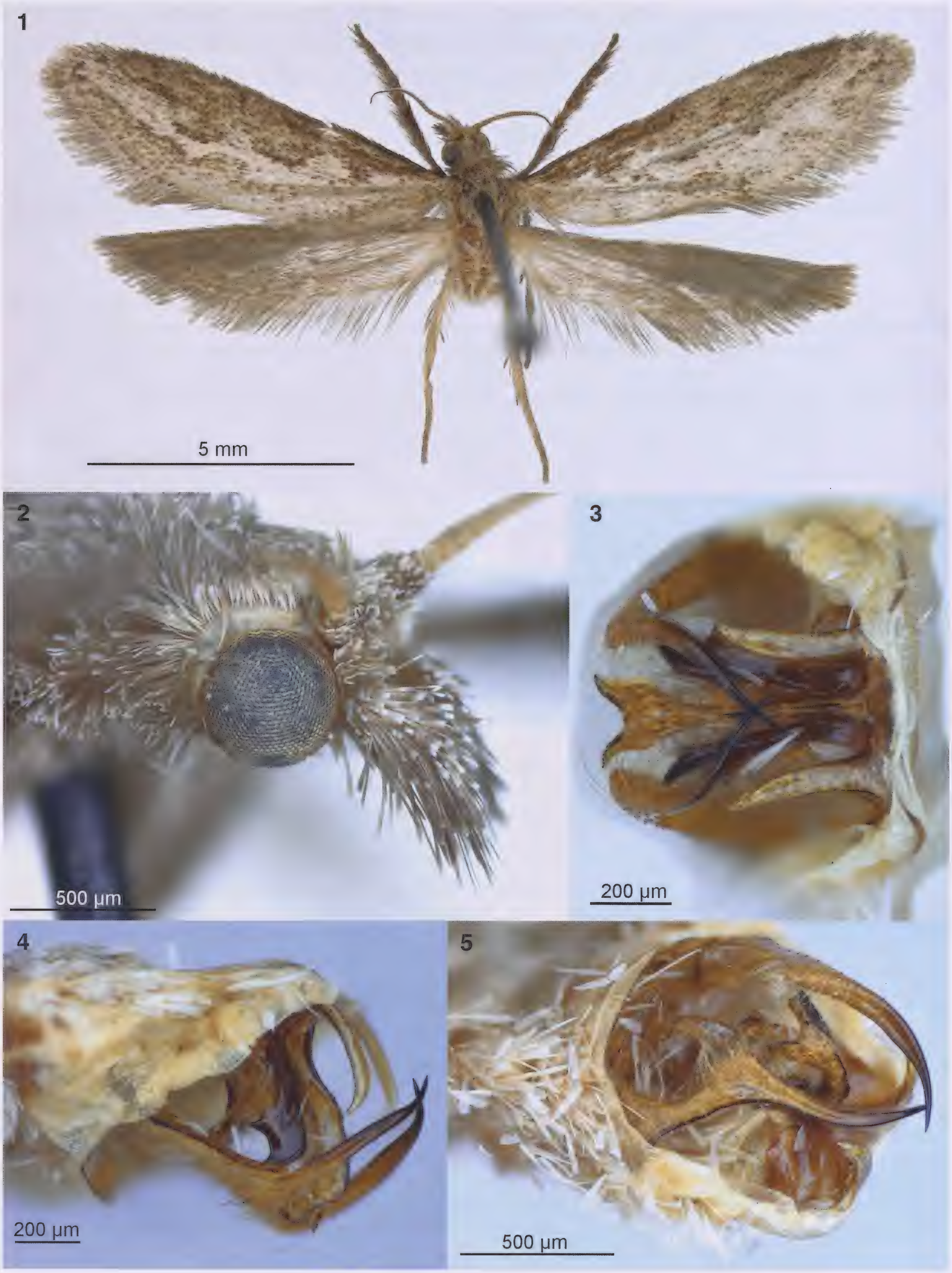


Figs 1-5. *Prototheora katangensis*, habitus and genitalia in situ of male holotype. (1) Habitus. (2) Head in lateral view. (3-5) Genitalia. (3) Apical view. (4) Lateral view. (5) Semi-ventral view.

Description

Male (Figs 1, 2): Head with scales between antennae and on frontoclypeus narrow, uniformly pale tan; posteriorly on vertex scales narrow, slightly longer, mixed light greyish brown with white tip and pale greyish white; on occiput with scales 2-3X as long as vertex scales, slender (some piliform), erect, greyish brown with white tip; without scales between eye margin and margin of antennal socket. Antenna with 26 flagellomeres, about 0.3X length of forewing, with pale brown to darker greyish brown, white-tipped scales dorsally only on scape, pedicel and first four flagellomeres, with fewer scales from pedicel to 3rd flagellomere; rest of flagellomeres' surface with short setae of same length from basal to apical flagellomeres. Labial palpus with vestiture expanded dorsoventrally, scales greyish brown, paler at base dorsally, usually white tipped. Thorax: Scales of dorsum of variable lengths and widths, those of undercover mostly uniformly white to dirty white, longer piliform scales greyish brown with white tip; basal half of metascutum devoid of scales, with tiny spines directed medially, posterior half with dirty white piliform scales directed posteromedially; ventrally with sparse vestiture of short white, appressed scales and long, light greyish brown, piliform scales. Wingspan 17 mm. Forewing length 8.0 mm; colour mostly dark brown on costal half with scales paler at their base, darker brown at base, pale brown on dorsal half, with white irregular stripe from base to apex below midline, running parallel to dorsum and termen, costa with short, uniformly colored scales of various shades of grey from base to before apical fringe scales; fringe pale greyish brown to white. Hindwing greyish brown, paler at base of dorsum, with concolourous fringe. Foreleg with short, brown, mostly white-tipped scales and longer, more slender, darker and longer greyish brown white-tipped scales slightly erect along dorsal margin of tibia and first three tarsomeres. Midleg as foreleg except with fewer and mostly paler, less-contrastingly patterned longer scales on dorsal margin of tibia and tarsomeres I-III, with some of these longer scales piliform. Hindleg with white to dirty white, mostly uniformly coloured scales, darker on last three tarsomeres, with few piliform on most segments. Abdomen colour not recorded.

Male genitalia (Figs 3-5, 11). Tegumen with an elongate, slender uncus arising medially from ventro-caudal margin of tegumen; apex of uncus bifurcate; a pair of slender tergal processes arising from dorso-caudal margin of tegumen; a pair of stout processes with slightly broader bifurcate apices arising ventrally from base of tegumen. Gnathos consisting of a slender sclerotized bridge extending between ventral processes of tegumen. Juxta moderately broadly triangular at base and then tapering to a much slender apex. Valvae elongate, slender and curved dorsad near midlength. Vinculum broad, with anterior margin slightly produced near middle; a slender, deeply bifurcate process projects middorsally from caudal margin of vinculum. Phallus membranous.

Female: Unknown.

Distribution: (Fig. 14). Known only from the type locality, which is located approximately 20 km west of Likasi, 20 km south of Kambove, and about 145 km northwest of Lubumbashi at 11°03′S 26°33′E (Wikipedia).

Remarks: The costal 1/3 of the hindwings of the unique specimen available is folded ventrally behind the rest of the hindwings. Jean Romieux (1893-1951), the collector of the holotype of *P. katangensis* was a mining engineer who worked in the Haut-Katanga province for several years in the 1920s and 1930s. He was also a prominent member of the "Société lépidoptérologique de Genève", which became the "Société entomologique de Genève" in 1946. Mr Romieux's collection was donated to the MHNG over the course of his life, as he worked there as an assistant occasionally (Rehfous, 1952). Seventy-two species, for which the holotypes are in the MHNG, have been described based on his beautiful material until now. The stout, elongate process that arises from the ventro-caudal margin of the tegumen in this species, has been referred to as the uncus in this study. A similar structure has not been observed in other *Prototheora*.

Prototheora tanzaniensis Davis & Landry sp. nov

Figs 6-10, 12-14

Material examined

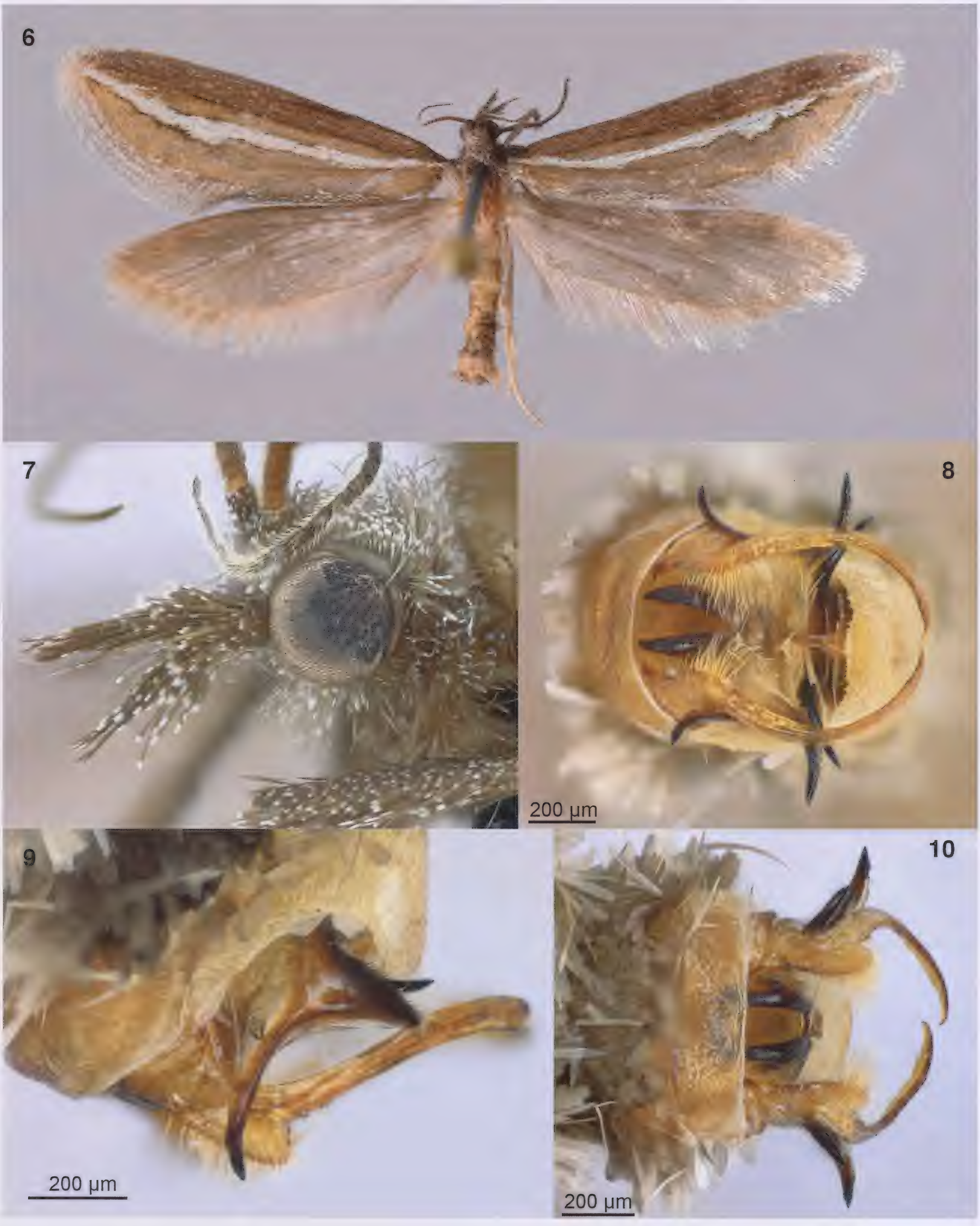
Holotype: ♂, 1- "TANZANIA | Iringa Reg[ion]., Makete Distr[ict].: | Kiitulo [sic] Plateau N[orth]. 2700 m | 29. xi. - 1. xii. 2005 | L. Aarvik, M. Fibiger, A. Kingston" (printed on white card stock in black ink); 2- "BL 1830 ♂" (green paper, hand written in black ink); 3- "♂ genitalia on | slide 4653 | D.R. Davis (printed except for hand-written number)"; 4- "HOLOTYPE | Prototheora | tanzaniensis | Davis & Landry" (hand written on red card stock in black ink) (NHMO).

Type locality: Tanzania, Iringa Region, Makete District, Kitulo Plateau North, 2700 m in elevation.

Diagnosis: This species is remarkable and distinct from its congeners by the golden yellow bands above and below a clearly contrasting white band on the forewing (Fig. 6).

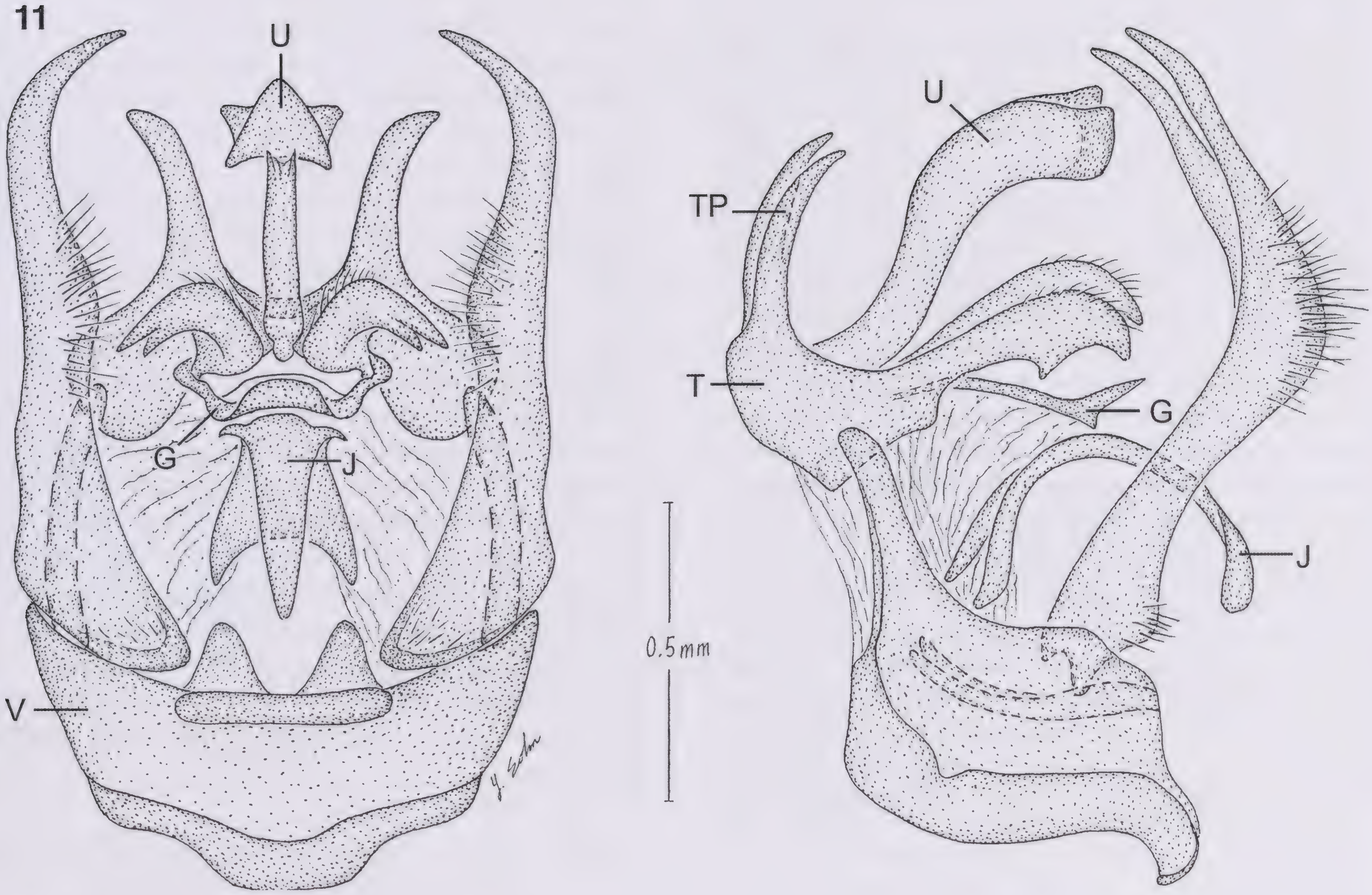
Description

Male (Figs 6, 7): Head with scales between antennae and on frontoclypeus short and mostly narrow, directed straight up, greyish brown with white tip; posteriorly on vertex with most scales similar, appressed and converging toward middle; on occiput with few erect piliform scales 2-3X as long as vertex scales, concolourous with those of rest of head; without scales between eye margin and margin of antennal socket. Antenna with 30 flagellomeres, about 0.3X length of forewing, with 2-3 dark greyish brown, white-tipped scales on first three flagellomeres and pedicel; rest of flagellomeres' surface with short

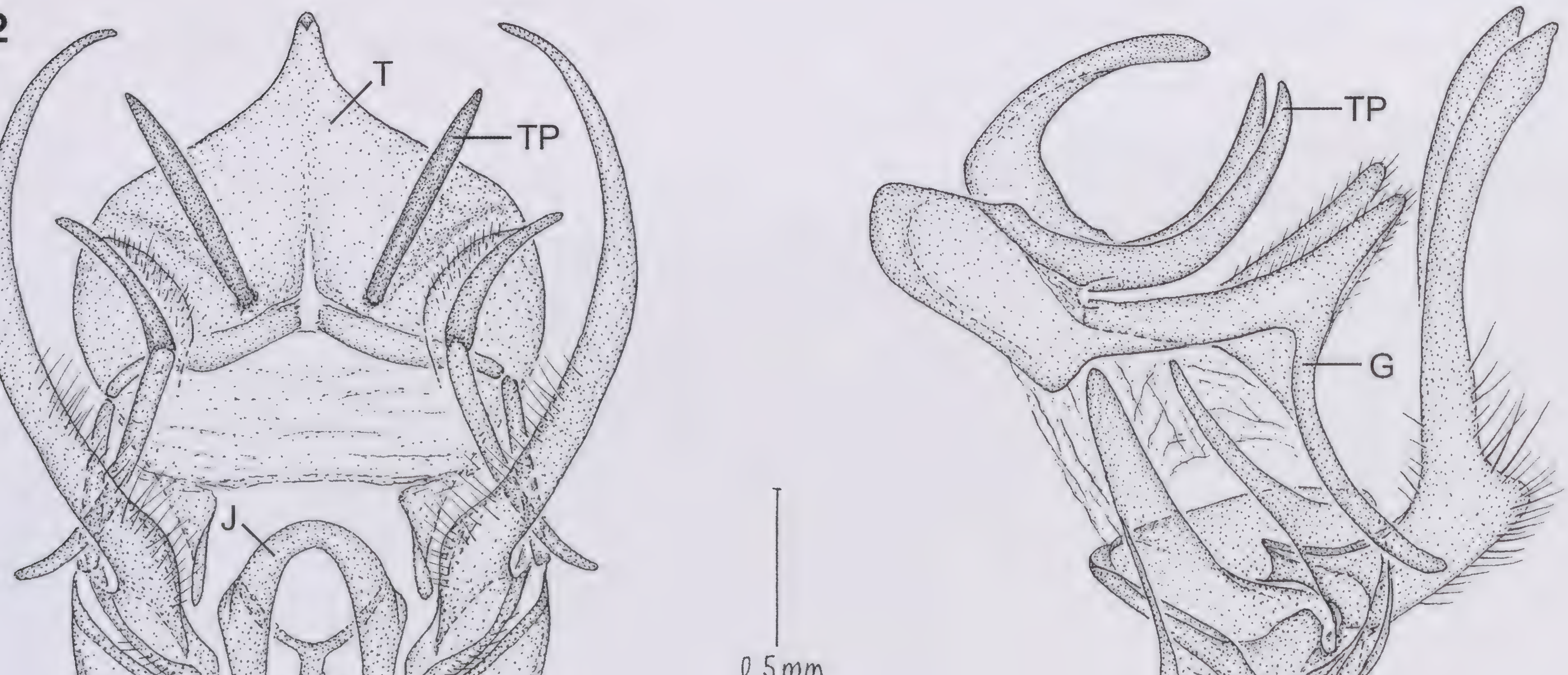


Figs 6-10. *Prototheora tanzaniensis*, habitus and genitalia in situ of male holotype. (6) Habitus. (7) Head in lateral view. (8-10) Genitalia. (8) Apical view. (9) Lateral view. (10) Ventral view.

11



12



Figs 11-12. Genitalia of *Prototheora* male holotypes in ventral view (left) and lateral view. (11) *P. katangensis*. (12) *P. tanzaniensis*. G: gnathos, J: juxta, T: tegumen, TP: tergal process, U: uncus, V: vinculum.

setae of equal length from basal to apical flagellomeres, about half as long as width of basal flagellomeres. Labial palpus slender, with scales white-tipped greyish brown. Thorax: Scales of dorsum greyish brown, darker at base of tegulae, with mixture of short, appressed, narrow scales and longer piliform scales; basal half of metascutum devoid of scales, with tiny spines directed medially, posterior half with dirty white piliform scales directed posteromedially; ventrally with sparse vestiture of short white, appressed scales and long, light greyish brown, piliform scales. Wingspan 21 mm. Forewing length 10.0 mm; with wide costal greyish brown band enclosing some white-tipped scales from middle and closer to costa; with white median band from base to apex running parallel to dorsum and termen, with single row of brown scales along most of its dorsal and ventral edges; with golden yellow above and below white band, with some white and greyish brown along dorsal margin from base to 2/5; with irregular terminal line of short white scales; fringe light greyish brown, white-tipped scaled. Hindwing light greyish brown with golden hue along costa from middle and along terminal and dorsal margins; fringe light golden at base, otherwise with scales white-tipped, light greyish brown. Foreleg dark greyish brown with most scales white tipped; with few longer and more slender, slightly erect scales along dorsal margins of tibia and first three tarsomeres. Midleg with scales mostly uniformly dark greyish brown on femur and base of tibia, lighter greyish brown to grey towards apex of tibia and on tarsomeres. Hindleg uniformly light greyish brown, with white only at apex of terminal tarsomere; with concolourous, uniformly coloured, erect piliform scales along dorsal and ventral margins of tibia. Abdomen colour not recorded.

Male genitalia (Figs 8-10, 12). Tegumen very broad, triangular, terminating in a slender, acute apex; a pair of slender, acute, and upturned tergal processes arising ventrally from tegumen. Gnathos comprised of a pair of slender, spinose sclerites arising ventrally from anterior margin of tegumen; median region of gnathos projecting ventro-caudally as an elongate, acute lobe. Juxta with slender arms in the form of an inverted U-shaped sclerite. Valvae elongate, slender, slightly broader at basal fifth where valva then turns abruptly dorsad at about a 45° angle. Vinculum broad, with anterior margin slightly curved and with a minute median indentation. Phallus membranous.

Female: Unknown.

Fig. 13. *Prototheora* habitat of male holotype of *P. tanzaniensis*, with collector of specimen Leif Aarvik, left, and Michael Fibiger†.

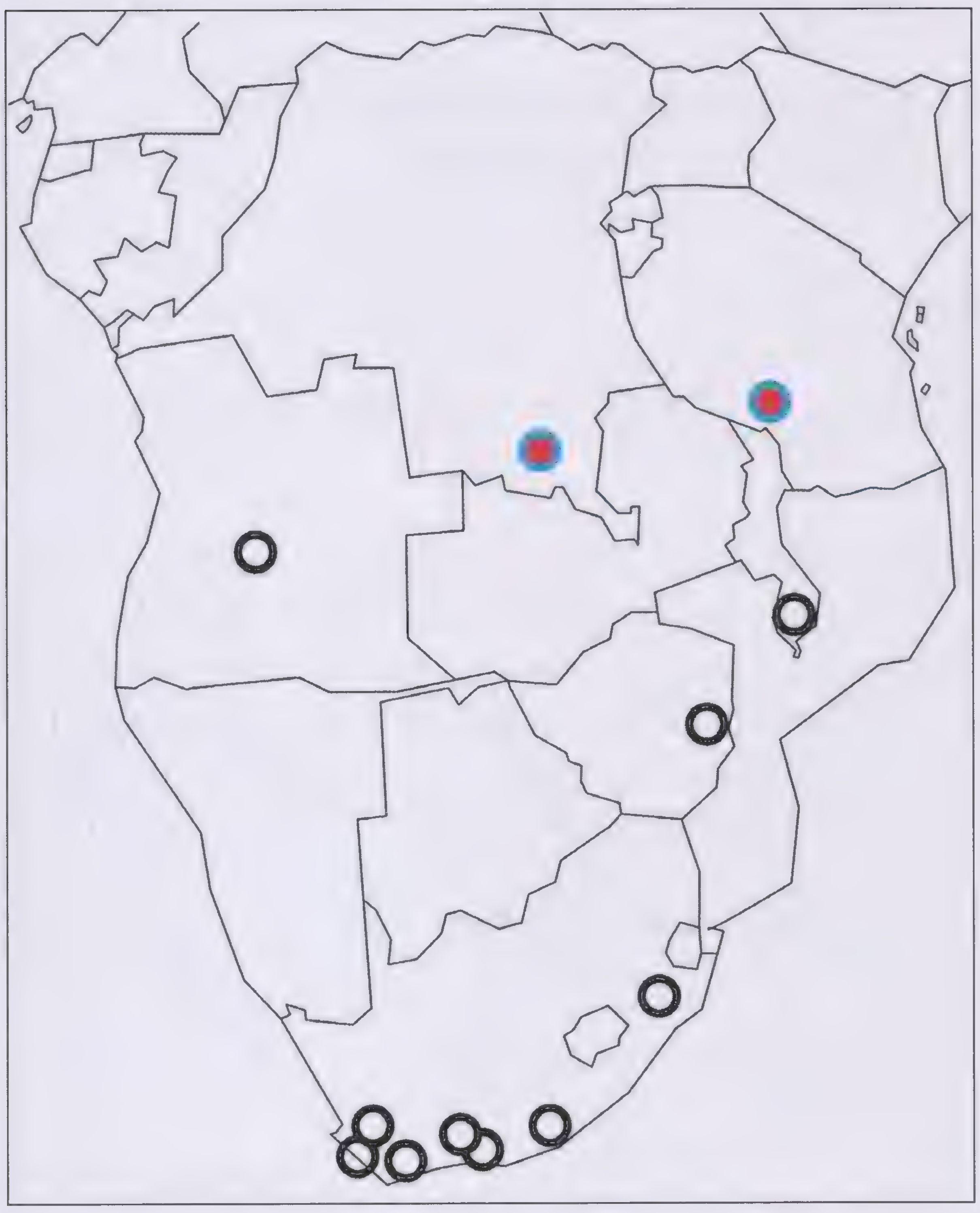


Fig. 14. Distribution map of all known *Prototheora* species in Africa with the coloured dots representing the collecting localities of the species described herein, modified from that of John Grehan (http://johngrehan.net/index.php/hepialidae/prototheoridae) with permission.

Distribution: (Fig. 14). Known only from the type locality in Tanzania.

Remarks: The holotype's right forewing is partly folded onto itself at the tip of the longitudinal white band, hence a break is visible on the outer margin of the wing. The correct spelling of the collecting locality's name of the Plateau is 'Kitulo'. The vegetation cover of the collecting locality is shown in Fig. 13.

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We are grateful to John Grehan (Evans, New York), for providing information and suggestions to improve our understanding of the species described here and to improve the manuscript, Leif Aarvik (NHMO) for the gracious loan of the unique holotype of *P. tanzaniensis*, Philippe Wagneur (MHNG) for the photo of the holotype of *P. tanzaniensis*, Florence Marteau (MHNG) for producing the plates, Young Sohn, Department of Entomology, NMNH, for the genitalia drawings, and J. Grehan, Gilles Roth (MHNG) and F. Marteau for the distribution map (Fig. 14).

REFERENCES

Davis D.R. 1996. A revision of the South African family Prototheoridae (Lepidoptera: Hepialoidea). *Insect Systematics & Evolution* 27(4): 393-439, 122 figs.

Davis D.R. 2001. A new species of *Prototheora* from Malawi, with additional notes on the distribution and morphology of the genus (Lepidoptera: Prototheoridae). *Proceedings of the Entomological Society of Washington* 103(2): 452-456.

Davis D.R. 2004. *Fasc. 11, Prototheoridae. In*: Heppner J. B. (ed.) Lepidopterorum Catalogus (New Series).

Mey W. 2017. A new species of *Prototheora* from Zimbabwe, with additional collecting records of the genus in South Africa (Lepidoptera: Hepialidae). *Metamorphosis* 28: 26-28.

Regier J.C., Mitter C., Kristensen N.P., Davis D.R., Van Nieukerken E.J., Rota J., Simonsen T.J., Mitter K.T., Kawahara A.Y., Yen S.-H., Cummings M.P., Zwick A. 2015. A molecular phylogeny for the oldest (nonditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life-history evolution. *Systematic Entomology* 40 (4): 671-704.
DOI: 10.1111/syen.12129

Rehfous M. 1952. † Jean Romieux, entomologiste, 1893-1951. *Bulletin de la Société entomologique suisse* 25(1): 56.

Simonsen T. J., Kristensen N. P. 2017. Revision of the endemic Brazilian 'neotheorid' hepialids, with morphological evidence for the phylogenetic relationships of the basal lineages of Hepialidae (Lepidoptera: Hepialoidea). *Arthropod Systematics & Phylogeny* 75(2): 281-301.

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A swimming medusoid gonophore in the life cycle of *Ventromma halecioides* (Alder, 1859) (Hydrozoa: Leptothecata: Kirchenpaueriidae)

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Abstract: The swimming gonophore of *Ventromma halecioides* (Alder, 1859) is described for the first time. It is a short-lived cryptomedusoid, provided with a well-formed, elongated-ovoid umbrella with thick mesoglea which, in turn, lacks a gastrovascular system, tentacles and tentacle bulbs, as well as sense organs. Its solid spadix is attached laterally to the blastostyle, and is surrounded by a compact mass of gametes, filling completely the subumbrellar cavity. The bell margin is provided with a raised collar comprising numerous refringent granules, and a velum is present. Scattered pseudostenoteles occur on exumbrella, while transversely-set muscle cells line the subumbrella.

Keywords: Life cycle - medusoid - cryptomedusoid.

INTRODUCTION

The production of swimming medusoid gonophores [for details, see Boero & Bouillon (1989)] among many "unusual" families of thecate hydroids is poorly documented and relatively misunderstood, as their occurrence is still unpredictable and often unexpected when it is discovered. To date, the presence of such a dispersive stage was already described in the lovenellid genus *Hydranthea* (Hincks, 1868) (Boero & Sarà, 1987), the hebellid genus *Anthohebella* Boero *et al*., 1997 (original account), the haleciid genus *Nemalecium* Bouillon, 1986 (Gravier-Bonnet & Migotto, 2000; Galea *et al*., 2012), the sertulariid genera *Amphisbetia* L. Agassiz, 1862 (Motz-Kossowska, 1907), *Sertularia* Linnaeus, 1758 (Migotto, 1998) and *Sertularella* Gray, 1848 (Gravier-Bonnet & Lebon, 2002), the plumulariid genera *Dentitheca* Stechow, 1919 (Migotto & Marques, 1999; Galea *et al*., 2012) and *Monotheca* Nutting, 1900 (Motz-Kossowska, 1907), the halopteridid genus *Antennella* Allman, 1877 (Bourmaud & Gravier-Bonnet, 2005), and the aglaopheniid genus *Macrorhynchia* Kirchenpauer, 1872 (Bourmaud & Gravier-Bonnet, 2004). Additional indications of occurrence of medusoids in other genera and/or species are scattered in the literature, and need to be confirmed through accurate observations.

The main obstacle to the discovery of swimming gonophores is, by far, the study of fixed material, followed by the disregard of histological studies. Except for the gonophores of *Hydranthea* and *Anthohebella*, all those described until now in the families mentioned above belong to the cryptomedusoid type [for definition and classification, see Bouillon *et al*. (2006)], characterized by the presence of a well-defined umbrella which, in turn, is devoid of tentacles and tentacle bulbs, gastro-vascular system, and sense organs. The spadix is eccentric, solid and, consequently, does not open distally into a mouth. The subumbrella is provided with muscle cells, and a velum is present in the majority of cases, allowing the gonophores to swim, although these appear to be likely absent in rare instances (Bourmaud & Gravier-Bonnet, 2005; Galea *et al*., 2012). In all but one family (*viz*. Sertulariidae), the bell margin bears a raised collar comprising a belt of refringent corpuscles whose function is not as yet totally understood, though it is possibly involved in the medusoid buoyancy. These bodies are labile in many fixatives, except perhaps the alcohol. Indeed, Kirchenpauer (1872: 16), noted – for the first time – their presence in nearly all species of *Macrorhynchia* he studied, but erroneously interpreted them as being oocytes. Additional observations by Bale (1894: 106; 1914: 30) and Allman (1883: 34) were likely done on alcohol-preserved specimens. The occurrence of refringent corpuscles in the gonophores is, most probably, a good indication of the production of swimming medusoids. However, their absence in the Sertulariidae could be an impediment even when working with living material, unless the spawning is monitored.

Leclère *et al*. (2009) have shown that swimming medusoid gonophores "are probably not secondary

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simplified medusae but simple pelagic forms re-acquired independently from polyp-only ancestors", provided with a set of morphological characters (*e.g.* umbrella with muscle cells, presence of a velum) gained subsequently after a previous lost.

Ventromma halecioides (Alder, 1859) is a well-known, nearly cosmopolitan species (Gravili *et al.*, 2015). Although its gonothecae were originally described and illustrated accurately by Alder (1859, pl. 12 fig. 4), the gonophore received lesser attention ("Pressed between plates of glass, the capsules showed the ova in a very early stage"). Some subsequent authors (*e.g.* Calder, 1997), reported the presence of fixed sporosacs, although Gravier-Bonnet & Migotto (2000) cite unpublished data of Migotto & Marques, according to which medusoids occur in this species.

Abundant, fertile colonies of this species were collected recently from the French coast of the Mediterranean Sea, allowing its reproduction to be documented.

MATERIAL AND METHODS

Colonies of *V. halecioides* growing on floating docks in the port of La Ciotat were collected by scraping. The material was brought to the laboratory in a cooler, within an hour. The colonies were placed in crystallizing dishes covered by a fine mesh, and immersed in two 5 L tanks filled with fresh seawater (from the collecting site) and supplied with aeration, either in the dark or exposed at the daylight, at *ca.* 25°C. The dishes were inspected every 15 minutes for the medusoid release under a Huvitz HSZ-TR30 trinocular stereomicroscope equipped with a Canon EOS 60D camera. Male and female individuals were immediately placed in separate dishes, and kept in the same conditions as stated above. Photomicrographs were taken using a Tucsen IS1000 CMOS (10 MPixel) camera mounted on a Optika B-500 trinocular compound microscope, with either transmitted light or darkfield illumination. The experiment was done four times. All studied material was subsequently fixed in Bouin's liquid, and part of it was transferred to 70% ethanol for long-term storage, while another part was stained in Grenacher's borax carmine according to the protocol given by Gibbons & Ryland (1989), and mounted on microslides. To test the tolerance of the refringent granules to the pH, 20 µL of a 1 M HCl or 1 M NaOH solutions were pipetted into the seawater containing a few medusoids placed on a depression slide covered with a coverslip, and their behavior was monitored under the microscope. Part of the material studied here was deposited in the collection of the *Muséum d'histoire naturelle* of Geneva, Switzerland (registration is indicated by MHNG-INVE- followed by a 5-digit number), while another part is housed in the private collection of the author (registered as HRG- followed by a 4-digit number).

RESULTS

Family Kirchenpaueriidae Stechow, 1921

Genus *Ventromma* Stechow, 1923

***Ventromma halecioides* (Alder, 1859)**

Figs 1-2

Plumularia halecioides Alder, 1859: 353, pl. 12.

Material examined: MHNG-INVE-99622; France, La Ciotat, old harbor, 43.172512° 5.610192°, 0-0.3 m; 05, 07 and 11 Sep. 2017; fertile colonies, detached stolonal gonothecae, and medusoids in alcohol. – HRG-1342; France, La Ciotat, old harbor, 43.172512° 5.610192°, 0-0.3 m; 01 Sep. 2017; fertile colonies, detached stolonal gonothecae, and medusoids mounted on slides.

Systematics: Evidence from molecular work (Leclère *et al.*, 2007, 2009; Moura *et al.*, 2008; Peña Cantero *et al.*, 2010; Maronna *et al.*, 2016) indicate that this species should be assigned to the genus *Ventromma*, which forms a monophyletic group, different from *Kirchenpaueria* Jickeli, 1883, within the family Kirchenpaueriidae. Unlike the latter, with which it has been synonymized by a number of authors (*e.g.* Bouillon, 1985; Ansín Agís *et al.*, 2001), *Ventromma* is morphologically characterized by the presence of nematophores protected by nematothecae (Fig. 1A). A comprehensive synonymy of *V. halecioides* is provided by Ansín Agís *et al.* (2001).

Description: For a description of this species, refer to Calder (1997). Billard (1903) documented the morphological variations of its trophosome. Migotto (1996) noted the presence of two distinct regions, delimited by a transverse constriction, in the hydranth, an observation made earlier by Goette (1907: 322, pl. 12 fig. 258), and confirmed by the present study (Fig. 1B); however, their respective functions could not be ascertained at this stage.

The present material is fully fertile, with both cauline and stolonal gonothecae containing gonophores at various stages of development. Since the specimens could not be kept alive for more than 12 hours, the development of their gonophores could not be studied sequentially. However, their life history could be traced based on the present observations, and by homology with other species whose similar life cycles are well-characterized.

Only gonothecae of one sex were borne on a given stem but, due to the high density of plumes and the likely occurrence of multiple colonies on the same substrate, it is impossible to state whether *V. halecioides* is a mono- or dioecious species. Male and female gonothecae are indistinguishable morphologically, although their respective gonophores are immediately identifiable under the stereomicroscope.

One large and, often, a second, basal and comparatively smaller gonophore occur per gonotheca (Fig. 1C). This is especially obvious when female gonothecae are

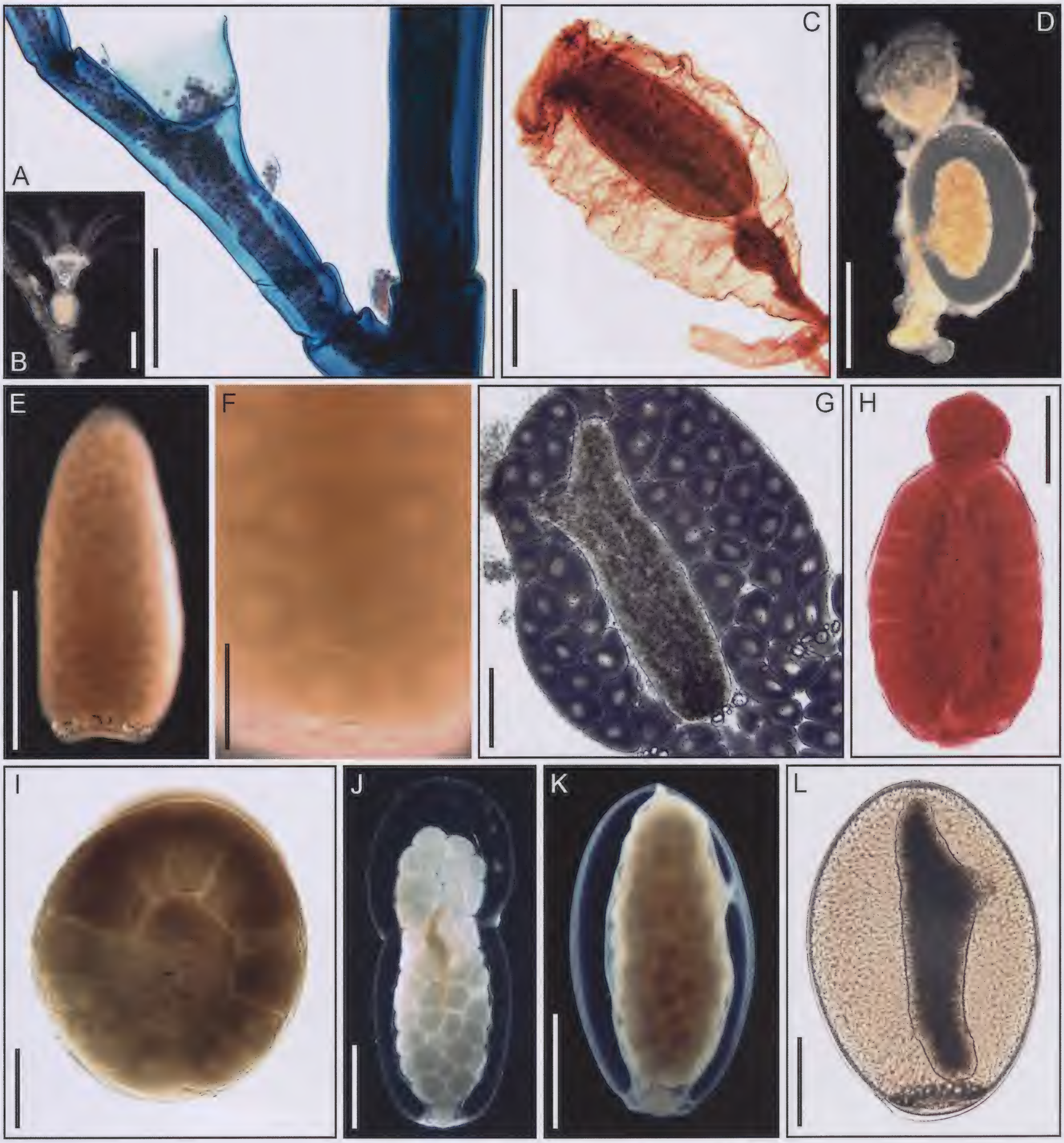

Fig. 1. (A) Portion of colony showing the cauline apophysis and its associated nematotheca, and proximal part of a cladium with first hydrothecate internode and its thecae. (B) Expanded hydranth, showing colors in life. (C) Gonotheca with female gonophore. (D) Whole young male gonophore extracted from its gonotheca. (E-F) Newly-liberated female medusoid (E) and close-up showing polygonal oocytes (F). (G) Squashed female medusoid showing Y-shaped spadix. (H-I) Stained (H) and cross-section (I) through female medusoid showing the spadix encircled by single layer of oocytes. (J-K) Female medusoid escaping from its protective membrane (J) and newly-liberated individual (K). (L) Male medusoid enveloped in membrane. Scale bars: 50 μm (B), 100 μm (A, F), 200 μm (C, G-I, L), 400 μm (D, E, J, K).

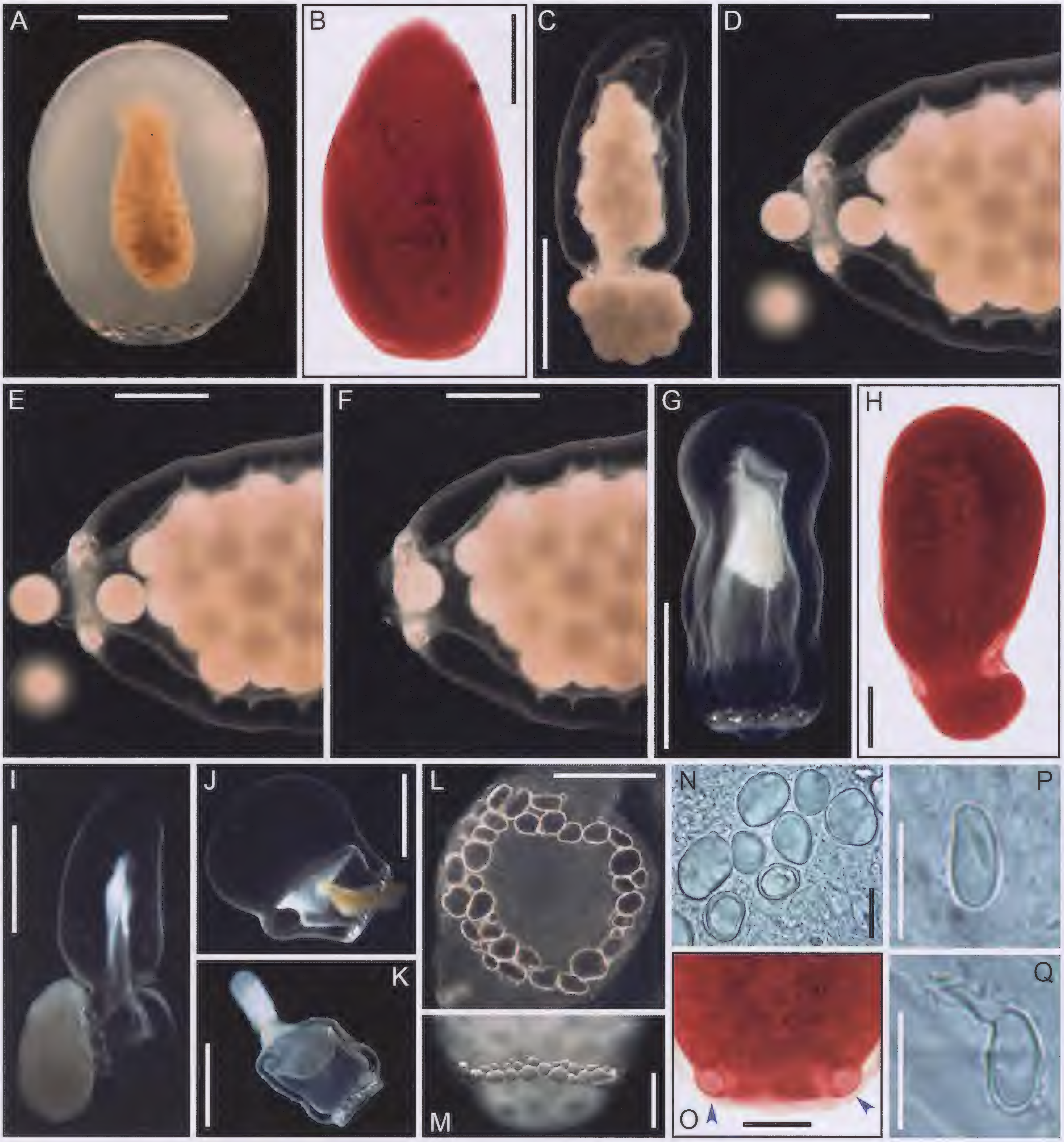

Fig. 2. (A-B) Male medusoid either showing colors in life (A), or stained (B) and displaying an Y-shaped spadix. (C) Partially spawned female medusoid with aggregate of oocytes. (D-F) Three steps of spawning (note presence of velum). (G) Emptied female medusoid. (H) Stained male medusoid partly liberating its gametes, showing directional arrangement of sperm cells. (I) Spawned male medusoid partly liberated from its membrane. (J, K) Spawned medusoids of unknown sex(es), the latter with the bell inside-out. (L-M) Belt of refringent corpuscles seen apically in a male medusoid (L) and laterally in a female (M). (N) Close-up of the refringent corpuscles. (O) Bell margin of a female medusoid showing large, vacuolated cells after the dissolution of the concretions (blue arrowheads). (P-Q) Pseudostenoteles from exumbrella either undischarged (P) or discharged (Q). Scale bars: 10 μm (P, Q), 20 μm (N), 100 μm (L, M, O), 200 μm (B, D-F, H), 400 μm (A, C, G, I-K).

examined, as the large oocytes are easily distinguishable from other cell types occurring in the gonophore. The main gonophore is budded off laterally from the lower half of a slender, tubular blastostyle running longitudinally from the proximal to the distal end of the gonotheca. In young thecae, the blastostyle ends up distally in a broad, globular, hollow apical plate (Fig. 1D), most likely involved in the building of the distal, and hence youngest, portion of the perisarcal sheet of the gonotheca. The more the gonotheca becomes morphologically complete and, simultaneously, its gonophore undergoes maturation, the more the apical plate becomes flattened (Fig. 1C), until it eventually disappears. Tall, columnar cells are easily noted on the side of the apical plate in contact with the inner gonothecal wall.

The very young gonophore is nearly spherical in shape and contains a globular spadix in its center (especially visible in males) linked laterally to the blastostyle. The latter assumes at this stage a sickle-shaped appearance, as it partly encircles the gonophore from one end to the other. A few conspicuous, refringent bodies form a belt towards the distal end of the gonophore. In males, the mass of spermatids is translucent while, in females, ovoid oocytes of various sizes encircle the spadix. The blastostyle, gonophore, and apical plate are enveloped together by a monostratified mantle. Numerous claw-like holdfasts emerge from the latter, anchoring – on one hand – the gonophore to the inner gonothecal wall, and – on the other hand – the border of the apical plate all the way around the insertion points of the future gonothecal operculum.

As the gonophore develops, it becomes gradually elongated, and its central spadix follows the same process. At these more advances stages, one can easily note that the brownish spadix is linked to the blastostyle through a lateral “arm” (Fig. 1D). In the female gonophores, the oocytes aggregate around the spadix into a single layer (Fig. 1H, I); they assume a polygonal (penta- or hexagonal) shape, their cytoplasm is translucid, allowing large nuclei with visible nucleoli to be noted (Fig. 1F, G). The number of refringent bodies increases gradually until a belt of up to 3 superimposed whorls is formed (Fig. 2L, M).

In more advanced male and female gonophores, a thin, transparent, unicellular membrane surrounding them, and distinct from the mantle, could be noted. It is likely that it is formed simultaneously with the gonophore, but its presence is indiscernible at earlier developmental stages, unless demonstrated by histological sections. It is composed of elongated cells, with large nuclei, arranged in parallel, intercalating rows. Among them, a few scattered pseudostenoteles occur [undischarged capsules (8.0-9.1) × (3.6-4.2) µm].

As the gonophores grow up in their already fully formed gonothecae, the apical plate regresses completely, leaving only the complex blastostyle-gonophore-mantle within the gonotheca. When fully formed, the gonophores escape from the gonotheca through a narrow, arc-shaped passage created by the partial cleave of the apical perisarc. All gonophores obtained during the four experiments carried out were liberated from their gonothecae still enclosed in their thin, transparent membrane (Fig. 1L). On the other hand, the jagged mantle and remains of the blastostyle remain trapped within the gonotheca. There was no apparent correlation between the medusoid liberation and the exposure of the colonies to light or dark, as a similar number of individuals were obtained in both cases.

The male gonophores subsequently undergo a change in the appearance of their content: from translucid, they become opaque, most probably upon the maturation of spermatids into sperm cells. Similarly so, the nuclei of the oocytes are no more visible, and the cells change in shape from polygonal to spherical (Fig. 1J). In a few instances, medusoids of both sexes were seen getting free (Fig. 1J), or already free (Fig. 1K), from their envelope. At this point, their mesoglea, previously thin and unnoticeable, expanded significantly and the gonophores adopted the characteristic shape of medusoids.

Structurally, they are true cryptomedusoids, as no radial or ring canals, no tentacles or tentacular bulbs, and no sense organs could be noted. A few pseudostenoteles (Fig. 2P, Q) are scattered on the exumbrella. The female medusoids are up to 1165 µm long and 655 µm wide, and produce up to 90 oocytes, while their male counterparts are up to 820 µm long and 585 µm wide. No natatory behavior has been ever observed after the liberation of the medusoids from their protecting membrane.

Spawning has been documented in a couple of female medusoids. An oocyte, whose diameter is *ca.* 110 µm, was released approximately every 2 minutes through a progressive contraction of the subumbrellar cavity, but not of the medusoid as a whole. Upon the passage of the oocytes through the bell aperture, the presence of a velum could be noted (Fig. 2D-F). The oocytes either fell individually to the bottom of the crystallizing dishes (Fig. 2D-F), or formed aggregates at the bell aperture (Fig. 2C). Male medusoids were not observed during the spawning, although one spent specimen (partially extracted from its envelope) was found (Fig. 2I). Similarly so, one spent female medusoid (Fig. 2G) was found in the crystallizing dish with female individuals. In addition, a couple of spent medusoids of unidentifiable sex(es) (Fig. 2J, K) were found among the hydroid colonies. One of them had its bell inside out (Fig. 2K), which allowed not only the presence of transverse muscle cells in the subumbrella to be noted, but also the absence of a mouth. The lack of the latter was also confirmed in the second spent medusoid, in which the spadix was partially extruded from the bell cavity (Fig. 2J). In addition, these two spent medusoids displayed jerking contractions of the bell, not noted in unspent individuals, probably due to the crowded condition of their gametes, completely filling the subumbrellar cavity. No correlation between the exposure to light or dark of the medusoids and their spawning was noted.

Table 1. List of species in which swimming medusoid gonophores presumably exist, or were described thoroughly.

Taxa	Reference(s)	Brief description and remarks
LOVENELLIDAE		
Hydranthea margarica (Hinks, 1863)	Motz-Kossowska (1911, as *Halecium billardi* sp. nov.); Boero & Sarà (1987: 134, fig. 5)	Spherical, 4 radial canals, ring canal, gonad surrounding the spadix, 8 statocysts, nematocysts scattered on exumbrella; no tentacles.
HEBELLIDAE		
Anthohebella brevitheca (Leloup, 1938)	Boero *et al*. (1997: 27, fig. 14)	Ovoid, 4 radial canals, 4 large atentaculate bulbs, velum present, spadix with 4 distinct interradial gonads, mouth present, striated muscles in subumbrella.
Anthohebella communis (Calder, 1991)	Galea (2013: 13, fig. 3R)	Male medusoids with 4 radial canals; no other details discernible in fixed gonothecae.
Anthohebella darwiniensis Watson, 2000	Watson (2000: 8, fig. 5D)	4 vestigial radial canals; 4 long rudimentary tentacles contracted into a wavy pattern; no velum or manubrium.
Anthohebella najimaensis (Hirohito, 1995)	Hirohito (1995: 131, as *Scandia najimaensis*); Boero *et al*. (1997: 28, fig. 16C-D)	Spadix surrounded by gonad, without radial canals, ring canal or marginal tentacles.
Anthohebella parasitica (Ciamician, 1880)	Boero (1980: 136, fig. 5, as *Hebella parasitica*); Boero *et al*. (1997: 25)	Ovoid, 4 radial canals, ring canal, 4 perradial bulbs with tentacle rudiments, 4 smaller interradial atentaculate bulbs, gonad encircling spadix, *ca*. 200 oocytes/medusoid. Presence of mouth invalidated subsequently (Boero & Bouillon, 1989; Boero, *pers. comm.*) Swim vigorously. Life span: 3-4 days under laboratory conditions.
Anthohebella tubitheca (Millard & Bouillon, 1973)	Boero *et al*. (1997: 27, fig. 15)	Ovoid, gonads around spadix, 4 radial canals.
HALECIIDAE		
Nemalecium lighti (Hargitt, 1924)	Bouillon (1986: 77, pl. 2 figs 2 & 4, pl. 3); Gravier-Bonnet & Migotto (2000: 208, figs 1-2)	Histological study done by Bouillon (1986), who demonstrates the occurrence of medusoids within the gonothecae, and noted the presence of a velum, most probably allowing the gonophore to become free and lead a short free life. Observational data on this species artificially mixed up with those of a putative undescribed species (see below) by Gravier-Bonnet & Migotto (2000). Colonies dioecious. Gonotheca opens apically. Medusoid elongated-ovoid, (1050-1400) × (420-550) µm, female producing 40-62 oocytes (120-135 µm wide). Mesoglea thick; exumbrella with scattered microbasic mastigophores; subumbrella with muscle cells. Bell margin provided with ring of large, ciliated cells enclosing one to more refringent corpuscles within large vacuoles. Velum present; active swimmers.
Nemalecium sp.	Gravier-Bonnet & Migotto (2000: 208, figs 1-2)	Observational data on this species and *N. lighti* artificially mixed up. Colonies either mono- or dioecious. Release at dawn. Medusoids similar to those of *N. lighti*.
Nemalecium gracile Galea *et al*. (2012)	Galea *et al*. (2012: 48, fig. 3)	Colonies and individual stems either mono- or dioecious. Gonophores liberated at sunset through rupture of apical perisarc of the gonotheca; elongated-ovoid, male (730-1085) × (255-340) µm, female (1025-1305) × (355-400) µm and carrying 30-35 oocytes. Mesoglea thick. A belt of refringent corpuscles in 1-3 whorls. Exumbrella with scattered pseudostenoteles. Subumbrella with muscle cells. Velum present.
SERTULARIIDAE		
Amphisbetia operculata (Linnaeus, 1758)	Teissier (1922: 358, figs 1-4, as *Sertularia operculata*), Motz-Kossowska (1907: cxvi, fig. 3, as *S. operculata*)	Liberated at night. Elongated-ovoid, spadix eccentric, females carrying *ca*. 50 oocytes 150-180 µm wide. Muscle cells on subumbrella; velum present, provided with muscle cells; active swimmers. Life span 10 minutes.
Sertularella diaphana (Allman, 1885)	Gravier-Bonnet & Lebon (2002: 105, fig. 1)	Observational data on this and following species reportedly similar and, consequently, pooled together. Colonies dioecious. Release at dawn through opening of gonothecal operculum. Medusoids bell-shaped, male (2157-2431) × 1200 µm, female (1875-2513) × (863-1313) µm and containing *ca*. 77 oocytes (*ca*. 184 µm wide). Mesoglea relatively thin, subumbrella with muscle cells. No nematocysts on exumbrella, no refringent corpuscles around bell aperture. Velum present; active swimmers. Spawning within 12 minutes after release.

Taxa	Reference(s)	Brief description and remarks
Sertularella sp.	Gravier-Bonnet & Lebon (2002: 105, fig. 1)	Putative undescribed species. Medusoids similar to those of *S. diaphana*; male (1765-2078) × (980-1375) μm, female (1875-2250) × (1188-1450) μm and containing 34-51 oocytes (*ca.* 235 μm wide).
Sertularia loculosa Busk, 1852	Unpublished data by Migotto cited by Gravier-Bonnet & Lebon (2002: 107)	Unpublished results.
Sertularia marginata Kirchenpauer, 1864	Migotto (1998: 5, fig. 2)	Colonies dioecious. Medusoid release after dusk, through narrow opening of gonothecal operculum; elongated-ovoid; male (852-1080) × (540-768) μm; female (960-1200) × (588-960) μm and producing 21-37 eggs. Mesoglea relatively thin; exumbrella with scattered microbasic mastigophores. No refringent corpuscles. Velum present; active swimmers.
Sertularia turbinata (Lamouroux, 1816)	Unpublished data by Migotto cited by Gravier-Bonnet & Lebon (2002: 107)	Unpublished results.
PLUMULARIIDAE		
Dentitheca asymmetrica (Bale, 1914)	Bale (1914: 30, as *Plumularia asymmetrica*)	"A cluster of rounded highly refractive granules near the aperture".
Dentitheca bidentata (Jäderholm, 1920)	Migotto (1997: 170), Migotto & Marques (1999: 956, fig. 4)	Colonies either mono- or dioecious. Gonophore ovoid, (720-940) × (500-720) μm. Mesoglea thick; exumbrella with scattered microbasic mastigophores; refringent corpuscles in 2-3 irregularly-concentric rings. Velum present; active swimmers. Spawning 15 min after release; life span *ca.* 2 hours. Females producing 10-12 oocytes (deduced from fig. 4C), 130-145 μm wide.
Dentitheca dendritica (Nutting, 1900)	Galea *et al.* (2012: 44, fig. 1)	Colonies dioecious. Medusoids liberated at sunset; ovoid to spherical, female *ca.* 550 × 240 μm and producing up to 20 oocytes (diameter 110-150 μm), male *ca.* 415 × 250 μm. Mesoglea thin; belt of refringent corpuscles. Presence of velum and/or muscle cells in the subumbrella could not be confirmed. Spawning within gonotheca. No contractions of the bell have been noted.
Monotheca obliqua (Johnston, 1847)	Motz-Kossowska (1907: cxv, figs 1-2, as *Plumularia obliqua*)	Only males documented. Elongated-ovoid. Muscle cells on subumbrella. A well-developed velum, though reportedly devoid of muscle cells, although spawning accompanied by contractions of the bell.
Monotheca margaretta Nutting, 1900	Unpublished data by Migotto & Marques, cited by Gravier-Bonnet & Migotto (2000: 212)	Unpublished results.
KIRCHENPAUERIIDAE		
Ventromma halecioides (Alder, 1859)	Unpublished data by Migotto & Marques, cited by Gravier-Bonnet & Migotto (2000: 212); present study	Individual stems dioecious. The gonothecal operculum opens only partially to allow the escape of the medusoid; the latter is elongated-ovoid, *ca.* 820 × 585 μm in males, and *ca.* 1165 × 655 μm in females, the latter producing up to 90 oocytes, *ca.* 110 μm in diameter. Exumbrella with scattered pseudostenoteles; subumbrella with muscle cells; velum present. Marked contractions of the bell observed after spawning.
HALOPTERIDIDAE		
Antennella sp.	Bourmaud & Gravier-Bonnet (2005: 56, figs 1-2)	Colonies monoecious. Medusoid not released from gonotheca; ovoid to nearly spherical; mesoglea thin; female producing *ca.* 5 oocytes. No muscle cells on subumbrella, no velum, no nematocysts on exumbrella. Spawning during the night.
AGLAOPHENIIDAE		
Aglaophenia latecarinata Allman, 1877	Unpublished data by Migotto & Marques, cited by Gravier-Bonnet & Migotto (2000: 212)	Unpublished results.
Aglaophenia sp.	Unpublished data by Boero & Bouillon, cited by Boero & Bouillon (1989: 37)	Putative undescribed species from Papua New Guinea. Spadix "displaced towards bell margin". No additional data available.
Gymnangium ascidioides (Bale, 1882)	Bale (1894: 106, pl. 5 fig. 1, as *Halicornaria ascidioides*)	"[...] a very distinct circle of highly refractive granules just below the aperture".
Gymnangium bryani (Nutting, 1906)	Ronowicz *et al.* (2017: 30)	"Gonophores with medusoid inside (release not observed)".
Gymnangium ferlusi (Billard, 1901)	Jarvis (1922: 355, fig. 5, as *Halicornaria ferlusi* var. *brevis*); unpublished data by Gravier-Bonnet, cited by Gravier-Bonnet & Migotto (2000: 212)	"The mouth is circular, surrounded by a double ring of highly refractive discs" (Jarvis, 1922).

Taxa	Reference(s)	Brief description and remarks
Gymnangium hians (Busk, 1852)	Unpublished data by Gravier-Bonnet, cited by Gravier-Bonnet & Migotto (2000: 212); Ronowicz *et al.* (2017: 30)	"Gonophores with free medusoids" (Ronowicz *et al.*, 2017).
Lytocarpia angulosa (De Lamarck, 1816)	Allman (1883: 34, pl. 20 fig. 3, as *Acanthocladium huxleyi*)	"gonophore [...] encircled just below its summit by a wreath of refringent spherules".
Macrorhynchia filamentosa (De Lamarck, 1816)	Kirchenpauer (1872: 43, pl. 2 fig. 21, as *Aglaophenia ligulata*); Kirchenpauer (1872: 44, pl. 2 fig. 23, as *Aglaophenia patula*)	Medusoids undoubtedly depicted in pl. 2 fig. 21 (as *A. ligulata*) and pl. 2 fig. 23 (as *A. patula*), with their characteristic belt of refringent corpuscles.
Macrorhynchia philippina Kirchenpauer, 1872	Kirchenpauer (1872: 17, Fig.; pl. 2 fig. 26, as *A. philippina*); Kirchenpauer (1872: 46, pl. 2 fig. 27, as *A. urens*); Bale (1888: 787, pl. 21 figs 6-7, as *Lytocarpus philippinus*); Gravier (1970: 255, fig. 1B, C); Watson (2000: 68, fig. 53D); Bourmaud & Gravier-Bonnet (2004: 368, figs 1-2)	Colonies monoecious. Gonotheca opens wide into two valves; release at dusk. Gonophore ovoid, *ca.* 1315 × 950 μm [deduced from fig. 1C in Gravier (1970)]; female producing *ca.* 40 oocytes. Mesoglea relatively thin; exumbrella with pigment cells and scattered microbasic mastigophores; subumbrella with muscle cells. Marginal belt composed of 2-3 whorls of refringent corpuscles, soluble in acid. Velum present; active swimmers. Spawning within 1-2 minutes; life span of the medusoid *ca.* 2 hours.
Macrorhynchia racemifera (Allman, 1883)	Allman (1883: 41, pl. 13 fig. 5, as *Lytocarpus racemiferus*)	"The gonophore occupies the centre of the gonangium, from whose walls it is separated by a clear space, across which may be seen a wreath of highly refringent spherules, by which the summit of the gonophore is encircled".
Macrorhynchia sp.	Unpublished data by Gravier-Bonnet, cited by Gravier-Bonnet & Migotto (2000: 212)	Any data available on this species from Madagascar.
Taxella eximia Allman, 1874	Allman (1876: 278, pl. 22 fig. 2, as *Halicornaria saccaria*)	"[...] sporosac encircled near its summit by a band of refringent roundish corpuscles".

As noted above, there is a belt of refringent bodies around the bell aperture in the medusoids of both sexes. Their shape ranges from nearly spherical to irregularly elongated, and their size varies from 10 to 33 μm long (Fig. 2N). They are likely of a mineral nature, and dissolve within less than 30 seconds in an acidic medium (though without obvious effervescence), but remain unaffected in an alkaline solution. Stained and mounted medusoids, in which the marginal bodies have dissolved, show an accumulation of quite large, polygonal cells around the bell margin that seem to delimit large "compartments" for housing these structures, possibly vacuolated cells. Two such diametrically opposed compartments may be mistakenly taken for a ring canal (Fig. 2O, arrowheads). Whether these compartments are represented by large, vacuolated cells could not be established at this stage, and a histological study is expected to clarify the case.

Remarks: The so-called "sketch of ring canal" noted by Bouillon (1986) in sections of medusoids of *N. lighti* likely correspond to the "ring of large cells enclosing [the] refringent corpuscles" observed by Gravier-Bonnet & Migotto (2000) in the same species. A similar histological structure may be also met with in the medusoid of *V. halecioides*, with the large "compartments" mentioned above corresponding to these vacuolated cells.

Watson (2011) created a new species, *V. bellarensis*, from southern Australia, and distinguished it from *V. halecioides* through the constant absence of ahydrothecate internodes on cladia. Given that her description was based on a single colony only and, taking into account that many authors (*e.g.* Naumov, 1969; Migotto, 1996; Ansín Agís *et al.*, 2001) described – besides the otherwise "distinctive" heteromerous segmentation of cladia – the occurrence of only hydrothecate internodes, or a combination of both, in *V. halecioides*, it is assumed that *V. bellarensis* is no more than a junior synonym of Alder's (1859) species.

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REFERENCES

Agassiz L. 1862. Contributions to the Natural History of the United States of America. Second monograph, vol. 4. *Little, Brown & Co., Boston*, 380 pp.

Alder J. 1859. Descriptions of three new species of sertularian zoophytes. *Annals and Magazine of Natural History* (3)3(17): 353-356.

Allman G.J. 1874. [Diagnosis of new genera and species of hydroids]. *Nature, London* 11(270): 179.

Allman G.J. 1876. Diagnoses of new genera and species of hydroids. *Journal of the Linnean Society of London. Zoology* 12: 251-284.

Allman G.J. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, Assistant United States Coast Survey. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 5(2), 1-66.

Allman G.J. 1883. Report on the Hydroida dredged by H.M.S. *Challenger* during the years 1873-76. Part I. – Plumularidae. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the year 1873-76, Zoology* 7(20): 1-55.

Allman G.J. 1885. Description of Australian, Cape, and other Hydroida, mostly new, from the collection of Miss H. Gatty. *Journal of the Linnean Society of London, Zoology* 19: 132-161.

Ansín Agís J., Ramil F., Vervoort W. 2001. Atlantic Leptolida (Hydrozoa, Cnidaria) of the families Aglaopheniidae, Halopterididae, Kirchenpaueriidae and Plumulariidae collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands. *Zoologische Verhandelingen, Leiden* 333: 1-268.

Bale W.M. 1882. On the Hydroida of south-eastern Australia, with descriptions of supposed new species, and notes on the genus *Aglaophenia*. *Journal of the Microscopical Society of Victoria* 2(1): 15-48.

Bale W.M. 1888. On some new and rare Hydroida in the Australian Museum collection. *Proceedings of the Linnean Society of New South Wales* 2(3)2: 745-799.

Bale W.M. 1894. Further notes on Australian hydroids, with descriptions of some new species. *Proceedings of the Royal Society of Victoria* 6: 93-117.

Bale W.M. 1914. Report on the Hydroida collected in the Great Australian Bight and other localities. *Fisheries. Zoological (and Biological) Results of the Fishing Experiments carried out by F.I.S. "Endeavour", 1909-1910* 2(1): 1-62.

Billard A. 1901. Note sur la *Polyplumaria flabellata* G.O. Sars et sur l'*Halicornaria ferlusi*. *Bulletin du Muséum d'Histoire naturelle de Paris* 7: 117-121.

Billard A. 1903. Note sur les variations du *Plumularia halecioides* Alder. *Bulletin du Muséum d'Histoire Naturelle de Paris* 9(1): 57-62.

Boero F. 1980. *Hebella parasitica* (Cnidaria, Hydrozoa): a thecate polyp producing an anthomedusa. *Marine Biology* 59: 133-136.

Boero F., Bouillon J. 1989. An evolutionary interpretation of anomalous medusoid stages in the life cycle of some Leptomedusae (Cnidaria) (pp. 37-41). *In:* Ryland J.S., Tyler P.A. (eds). Reproduction, Genetics and Distributions of Marine Organisms: 23rd European Marine Biology Symposium, School of Biological Sciences, University of Wales, Swansea. *Olsen & Olsen, Fredensborg, Denmark*, 469 pp.

Boero F., Sarà M. 1987. Motile sexual stages and evolution of Leptomedusae (Cnidaria). *Bollettino di Zoologia* 54: 131-139.

Boero F., Bouillon J., Kubota S. 1997. The medusae of some species of *Hebella* Allman, 1888, and *Anthohebella* gen. nov. (Cnidaria, Hydrozoa, Lafoeidae), with a world synopsis of species. *Zoologische Verhandelingen, Leiden* 310: 1-53.

Bouillon J. 1985. Essai de classification des Hydropolypes-Hydroméduses (Hydrozoa-Cnidaria). *Indo-Malayan Zoology* 1: 29-243.

Bouillon J. 1986. *Nemalecium* gen. nov., genre nouveau de Haleciidae (Thecata-Leptomedusae, Hydrozoa, Cnidaria). *Indo-Malayan Zoology* 3(1): 71-80.

Bouillon J., Gravili C., Pagès F., Gili J.M., Boero, F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle, Paris* 194: 1-591.

Bourmaud C., Gravier-Bonnet N. 2004. Medusoid release and spawning of *Macrorhynchia philippina* Kirchenpauer, 1872 (Cnidaria, Hydrozoa, Aglaopheniidae). *Hydrobiologia* 530/531: 365-372.

Bourmaud C. & Gravier-Bonnet N. 2005. Non-released cryptomedusoid in the life cycle of *Antennella* sp. (Cnidaria, Hydrozoa, Halopterididae) from La Réunion, Indian Ocean. *Invertebrate Reproduction and Development* 48(1-3): 55-62.

Busk G. 1852. An account of the Polyzoa, and sertularian zoophytes collected in the voyage of the "Rattlesnake" on the coast of Australia and the Louisiade Archipelago, etc. (pp. 343-402). *In:* Macgillivray J. (ed). Narrative of the voyage of H.M.S. Rattlesnake, commanded by the late Captain Owen Stanley, R.N., F.R.S. &c. during the years 1846-1850. Including discoveries and surveys in New Guinea, the Louisiade Archipelago, etc. To which is added the account of Mr. E.B. Kennedy"s expedition for the exploration of the Cape York Peninsula. Vol. 1. *Boone T. & W., London*, 402 pp.

Calder D.R. 1991. Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea. *Royal Ontario Museum Life Sciences Contributions* 154: 1-140.

Calder D.R. 1997. Shallow-water hydroids of Bermuda: superfamily Plumularioidea. *Royal Ontario Museum Life Sciences Contributions* 161: 1-84.

Ciamician J. 1880. Ueber *Lafoëa parasitica* n. sp. *Zeitschrift für wissenschaftliche Zoologie* 33(4): 673-676.

De Lamarck J.B.M. 1816. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractères essentiels de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Tome 2. *Verdière, Paris*, 568 pp.

Galea H. R. 2013. New additions to the shallow-water hydroids (Cnidaria: Hydrozoa) from the French Lesser Antilles: Martinique. *Zootaxa* 3686(1): 1-50.

Galea H.R., Ferry R., Bertot J.M. 2012. Medusoids in the life cycle of *Dentitheca dendritica* (Nutting, 1900) and *Nemalecium gracile* sp. nov. (Cnidaria: Hydrozoa). *Zootaxa* 3527: 43-54.

Gibbons M.J., Ryland J.S. 1989. Intertidal and shallow water hydroids from Fiji. I. Athecata to Sertulariidae. *Memoirs of the Queensland Museum* 27(2): 377-432.

Goette A. 1907. Vergleichende Entwicklungsgeschichte der Geschlechtsindividuen der Hydropolypen. *Zeitschrift für Wissenschaftliche Zoologie* 87: 1-335.

Gravier N. 1970. Libération de médusoïdes par *Macrorhynchia philippina* Kirchenpauer, 1872 (Hydroida, Plumulariidae). *Recueil des Travaux de la Station Marine d'Endoume. Fascicule hors-série suppl.* 10: 253-257.

Gravier-Bonnet N., Lebon M.L. 2002. Swimming medusoid gonophores in two species of *Sertularella* (Cnidaria, Hydrozoa, Sertulariidae) from Reunion Island, Indian Ocean. *Invertebrate Reproduction and Development* 41(1-3): 101-108.

Gravier-Bonnet N., Migotto A.E. 2000. Gonangium develop-

ment and medusoid of *Nemalecium lighti* (Hargitt, 1924) (Cnidaria, Hydrozoa, Haleciidae). *Scientia Marina* 64 (Suppl. 1): 207-213.

Gravili C., De Vito D., Di Camillo C.G., Martell L., Piraino S., Boero F. 2015. The non-siphonophoran Hydrozoa (Cnidaria) of Salento, Italy with notes on their life-cycles: an illustrated guide. *Zootaxa* 3908(1): 1-187.

Gray J.E. 1848. List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals. *Trustees of the British Museum, London*, 173 pp.

Hargitt C.W. 1924. Hydroids of the Philippine Islands. *Philippine Journal of Science* 24(4): 467-507.

Hincks T. 1863. On some new British hydroids. *Annals and Magazine of Natural History* (3)11(8): 45-47.

Hincks T. 1868. A history of British hydroid zoophytes. *John van Voorst, London*, LXVIII+338 pp.

Hirohito, Emperor of Japan. 1995. The hydroids of Sagami Bay. II. Thecata. *Publications of the Biological Laboratory, Imperial Household, Tokyo*, 244 pp.

Jäderholm E. 1920. On some exotic hydroids in the Swedish Zoological State Museum. *Arkiv för Zoologi* 13(3): 1-11.

Jarvis F.E. 1922. The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. *Transactions of the Linnean Society of London, Zoology* (2)18(1): 331-360.

Jickeli C.F. 1883. Der Bau der Hydroidpolypen. II. Über den histiologischen Bau von *Tubularia* L., *Cordylophora* Allm., *Cladonema* Duj., *Coryne* Gärtn., *Gemmaria* M'Crady, *Perigonimus* Sars, *Podocoryne* Sars, *Camponopsis* Claus, *Lafoëa* Lam., *Campanularia* Lam., *Obelia* Pér., *Anisocola* Kirchenp., *Isocola* Kirchenp., *Kirchenpaueria* Jick. *Morphologisches Jahrbuch* 8: 580-680.

Johnston G. 1847. A history of the British zoophytes. Vol. 1. Second edition. *Van Voorst, London*, VIII + 488 pp.

Kirchenpauer G.H. 1864. Neue Sertulariden aus verschiedenen Hamburgischen Sammlungen, nebst allgemeinen Bemerkungen über Lamouroux's Gattung *Dynamena*. *Verhandlungen der Kaiserlichen Leopoldino-Carolinischen deutschen Akademie der Naturforscher* 30: 1-16.

Kirchenpauer G.H. 1872. Ueber die Hydroidenfamilie Plumularidae, einzelne Gruppen derselben und ihre Fruchtbehälter. I. *Aglaophenia*, Lx. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg* 5(3): 1-58.

Lamouroux J.V.F. 1816. Histoire des polypiers coralligènes flexibles vulgairement nommés zoophytes. *F. Poisson, Caen*, 560 pp.

Leclère L., Schuchert P., Manuel M. 2007. Phylogeny of the Plumularioidea (Hydrozoa, Leptothecata): evolution of colonial organization and life cycle. *Zoologica Scripta* 36: 371-394.

Leclère L., Schuchert P., Cruaud C., Couloux A., Manuel M. 2009. Molecular phylogenetics of Thecata (Hydrozoa, Cnidaria) reveals long term maintenance of life history traits despite high frequency of recent character changes. *Systematic Biology* 58(5): 509-526.

Leloup E. 1938. Quelques hydropolypes de la baie de Sagami, Japon. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 14(28): 1-22.

Linnaeus C. 1758. Systema naturae per regna tria natura, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. *L. Salvii, Holmiae*, 823 pp.

Maronna M.M., Miranda T.P., Peña Cantero A.L., Barbeitos M.S., Marques A.C. 2016. Towards a phylogenetic classification of Leptothecata (Cnidaria, Hydrozoa). *Nature, Scientific Reports* 6, 18075. http://dx.doi.org/10.1038/srep18075

Migotto A.E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306: 1-125.

Migotto A.E. 1997. Aspects of the reproduction of *Denthiteca bidentata* (Cnidaria, Hydrozoa): a monoic plumulariid that releases medusoids. *Resumos expandidos do VII Congresso Latino-Americano sobre ciencias do mar* 2: 170-171.

Migotto A.E. 1998. The life cycle of *Sertularia marginata* Kirchenpauer, 1864 (Cnidaria: Hydrozoa: Sertulariidae): a medusoid-producing sertulariid. *Journal of Natural History* 32: 1-12.

Migotto A.E., Marques A.C. 1999. Redescription of *Dentitheca bidentata* (Cnidaria: Hydrozoa, Plumulariidae), with notes on its life cycle. *Journal of Natural History* 33: 949-960.

Millard N.A.H., Bouillon J. 1973. Hydroids from the Seychelles (Coelenterata). *Annales du Muséum royal de l'Afrique Centrale* 206: 1-105.

Motz-Kossowska S. 1907. Sur les gonophores de *Plumularia obliqua* Saunders et *Sertularia operculata* L. *Archives de Zoologie Expérimentale et Générale* (4)7(notes et revue 4): cxiv-cxviii.

Motz-Kossowska S. 1911. Contribution à la connaissance des hydraires de la Méditerranée occidentale. II. – Hydraires calyptoblastiques. *Archives de Zoologie Expérimentale et Générale* (5)6(10): 325-352.

Moura C.J., Harris D.J., Cunha M.R., Rogers A.D. 2008. DNA barcoding reveals cryptic diversity in marine hydroids (Cnidaria, Hydrozoa) from coastal and deep-water environments. *Zoologica Scripta* 37: 93-108.

Naumov D.V. 1969. Hydroids and hydromedusae of the USSR. Translated from Russian. *Israel Program for Scientific Translation, Jerusalem*, V + 631 pp.

Nutting C.C. 1900 American hydroids. Part I. The Plumularidae. *Special Bulletin of the United States National Museum* 4(1): 1-285.

Nutting C.C. 1906. Hydroids of the Hawaiian Islands collected by the Steamer Albatross in 1902. *Bulletin of the United States Fish Commission* 23(3): 931-959.

Peña Cantero A.L., Sentandreu V., Latorre, A. 2010. Phylogenetic relationships of the endemic Antarctic benthic hydroids (Cnidaria, Hydrozoa): what does the mitochondrial 16S rRNA tell us about it? *Polar Biology* 33(1): 41-57.

Ronowicz M., Boissin E., Bourmaud C.A.F., Gravier-Bonnet N., Schuchert P. 2017. Modern alongside traditional taxonomy – Integrative systematics of the genera *Gymnangium* Hincks, 1874 and *Taxella* Allman, 1874 (Hydrozoa, Aglaopheniidae). *PLOS One*. http://doi.org/10.1371/journal.pone.0174244

Stechow E. 1919. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. *Münchener medizinischer Wochenschrift* 1919(30): 1-37.

Stechow E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertebraten. *Archiv für Naturgeschichte* (A)87(3): 248-265.

Stechow E. 1923. Zur Kenntnis des Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zoologische Jahrbücher* 47(1): 29-270.

Teissier G. 1922. Observations des médusoïdes libres et des

planulas de *Sertularia operculata* L. *Bulletin de la Société Zoologique de France* 47: 357-361.

Watson J.E. 2000. Hydroids (Hydrozoa: Leptothecata) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museum and Art Galleries of the Northern Territory* 16: 1-82.

Watson J.E. 2011. New species, new records and redescriptions of thecate hydroids (Cnidaria: Hydrozoa: Leptothecata) from Southern Australia. *Zootaxa* 3122: 1-36.

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The woodlice (Crustacea: Isopoda) described by Henri de Saussure and Jean Carl

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Abstract: Henri de Saussure and Jean Carl were both prolific taxonomists who worked on many groups. Both paid some attention to the terrestrial isopods, although neither was mainly concerned with the order Isopoda. The Muséum d'histoire naturelle de Genève contains type specimens of nine species described by Saussure and eleven species or subspecies described by Carl. All of the species described by the two are enumerated, the presence of type specimens is noted and the current nomenclatural combination for each species is given.

Keywords: Woodlice - Oniscidea - Geneva - type catalogue.

INTRODUCTION

The Isopoda collection of the Muséum d'histoire naturelle de Genève (MHNG) is comparatively small but nonetheless rich in types. The early collections were rather limited, but the focus of more recent research on soil and cave faunas has resulted in a broad collection of the terrestrial Isopoda, albeit with an emphasis on the Palearctic region.

The Isopoda were among the groups collected by Henri de Saussure (1829-1905) during his expedition to the Antilles and Mexico in 1854-1856. Saussure worked on many groups including Hymenoptera, Orthoptera, Myriapoda and Crustacea (Hollier & Hollier, 2013), and described nine species of terrestrial Isopoda collected on his expedition. His exploration of cave faunas in Cuba marks the beginning of the long tradition of biospeleological research associated with the MHNG. Only one of the nine species described by Saussure is still valid. Saussure's specimens were originally directly pinned, but later card-mounted, and are still stored as dry specimens; although there are few labels on the pins, the other labels in the box provide important metadata allowing the specimens to be identified as types (see Fig. 1). Labels identifying specimens as syntypes have been added to the pins of the relevant specimens.

Jean Carl (1877-1944), assistant, curator and then deputy director at the MHNG from 1900 to 1944, followed Saussure in working on a variety of groups including the Orthoptera, Myriapoda and Crustacea. He also pioneered the study of cave and soil arthropods in Switzerland and founded the MHNG collection of Collembola. For his study of the Swiss isopod fauna Carl examined the collections in the museums of Basle, Bern, Frauenfeld and Neuchâtel, as well as collecting in the field (Carl, 1908a). He made extended trips to Ticino in 1905 and 1907, concentrating particularly on caves. He was accompanied on these trips by Angelo Ghidini (1876-1916), who knew the region and was employed as his assistant (Carl, 1908a). Carl also studied specimens from the collection of Adrien Dollfus (1858-1921), himself a specialist on Isopoda. Dollfus' collection was eventually deposited in the Muséum national d'histoire naturelle in Paris (MNHN). Carl described sixteen species or subspecies of Isopoda, ten of which are currently valid. His monograph on the Swiss Isopoda (Carl, 1908a) was awarded the Schläfli prize. Most of Carl's type specimens are stored in alcohol, although many samples collected for his work on the Swiss fauna are now dry and may have always been.

More recently specimens from the MHNG Isopoda holdings have been studied by experts including Albert Vandel, Claudio Manicastri, Stefano Taiti, Franco Ferrara and Helmut Schmalfuss, all of whom have deposited type specimens in the collection.

CATALOGUE

The species are listed alphabetically and the type locality and type series information from the original description are given. Nomenclature for the current combinations follows Schmalfuss (2003).

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Fig. 1. Isopoda collected by Henri de Saussure in Mexico and the Antilles. Photograph Philippe Wagneur.

albidus gallicus Carl, 1908b: 196-197, fig. 3 [*Trichoniscus*].
Cueva de Orobe [Spain] (coll. E. Simon). One ♂.
No specimens found in the MHNG. The holotype is presumably in the MNHN where Simon's collection is deposited.
A junior synonym of *Trichoniscoides cavernicola* (Budde-Lund, 1885)

albidus helveticus Carl, 1908a: 143-145, figs 43-46 [*Trichoniscus*].
Zürichberg, Frauenfeld, Genf, Crête du Locle [Switzerland]. More than one ♂ and ♀.
This taxon was raised to species level by Carl (1911: 25). The MHNG collection contains five specimens in alcohol, in two vials, under the name *Trichoniscus helveticus*. One vial, with one ♂ and three ♀ according to the label, has the locality "Zürichberg" and the date 11.X.05. The other specimen is without a precise locality, but the identification label is in Carl's handwriting and there is a typed label reading "coll. Carl." The specimens in the first vial are syntypes and it seems likely that the other specimen is as well.
Trichoniscoides helveticus (Carl, 1908)

aztecus Saussure, 1857: 307 [*Porcellio*].
Mexique. Unspecified series.
Saussure (1858: 479) gave the more precise locality "Cordova, terres chaudes du Mexique". The MHNG has five card-mounted specimens under the name "mexicanus (Aztecus Sss.)", the specimens having originally been directly pinned. The species name label in the box has "Amer. centr., M H de Sauss." handwritten on it. Two of the specimens have a small printed label "Cordova t.c." and are syntypes, while the others have a small printed label "Haiti" and are therefore not part of the type series.
Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

carinulatus Saussure, 1857: 308 [*Pseudarmadillo*].
Mexique ou l'île de Cuba. Unspecified series.
The MHNG collection has one card-mounted specimen

under this name. The specimen was originally directly pinned and although it has a small printed label "Cuba" and "Cuba, M H de Saussure" handwritten on the species name label in the box: Saussure (1858: 484) stated that he could not remember the provenance. This specimen is a syntype. Crustacea box 20.
Pseudarmadillo carinulatus Saussure, 1857

cavicolus Carl, 1906: 604-604, figs 1-6 [*Mesoniscus*].
Höhle bei Tre Crocette, am Campo de Fiore ob Varese [Italy]. Unspecified number of ♂.
The MHNG has thirteen specimens in alcohol, in two tubes, under this name. One tube, with eleven specimens, has a typed label "Mesoniscus cavicolus, Carl, grotto Tre Crocette, Campo dei Fiori, Varese, Italie, mat. Carl". These specimens are syntypes, despite the modern label. The other tube, with two specimens, is labelled "Grotta di Val Gamma 5.8.07" and as they were collected after the original description the specimens are not part of the type series.
A junior synonym of *Mesoniscus alpicola* (Heller, 1858)

coecum Carl, 1904: 327-329, figs 9-11 [*Ligidium*].
Höhle Kisil, Krim [Russia/Ukraine]. More than one specimen (size given as range).
The MHNG collection contains six specimens in alcohol, in two vials, under this name. The localities, handwritten on the identification labels, are "Grottes de la Crimée" and "Crimée, grottes, Carl" and the specimens are syntypes.
Typhloligidium coecum (Carl, 1904)

cotillai Saussure, 1857: 307 [*Porcellio*].
Cuba. Unspecified series.
Saussure (1858: 497) gave the type locality as "à l'entrée de la Grotte de Cotilla à huit lieues de la Havane". The MHNG collection includes two specimens under this name; both are card-mounted, having originally been directly pinned. One has a small printed label with "Cuba", the other is without labels. The species name label in the box has "Cuba, M H de Saussure" handwritten on it, and the specimens are syntypes. Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

cristallinus Carl, 1906: 607 [*Leucocyphoniscus*].
Grotta dell'Alabastro am Mte Generoso [Switzerland]. Two ♂.
Carl (1908a) mentioned further specimens, including ♀ specimens, from the Böggia cave near Meride in Ticino, Switzerland. The MHNG collection contains 16 specimens in alcohol under this name. They are in two vials, one with five specimens has the locality "Tessin mérid." and "Grotte Meride" on the identification labels, the other, with 11 specimens, has the locality "Böggia bi Meride" and the date 8.IX.07. These are not part of the type series, and the whereabouts of the two syntypes is unknown.

A junior synonym of *Leucocyphoniscus verruciger* Verhoeff, 1900

cubensis Saussure, 1857: 306 [*Armadillo*].
Cuba. Unspecified series.
Saussure (1858: 482) gave the more precise locality "à l'entrée de la grotte de Cotilla, non loin de la Havane". The MHNG collection has four card-mounted specimens, originally directly pinned, under this name. The species name label in the box has "Cuba, M H de Saussure" handwritten on it. Three of the specimens have a small printed label "Cuba" and are syntypes, while the fourth has a small handwritten label "Mexico" and is therefore not a syntype. Crustacea box 20.
A junior synonym of *Cubaris murina* Brandt, 1833

cubensis Saussure, 1857: 307 [*Porcellio*].
Cuba. Unspecified series.
The MHNG has one card-mounted specimen under this name. The species name label in the box has "Cuba, M H de Saussure" handwritten on it and the specimen has a small printed label "Cuba". This specimen is a syntype. Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

dollfusi Carl, 1908b: 171-172, fig. 1 [*Leucocyphoniscus*].
Grottes de Choranche (Isère), Caves de Saint-Nazaire-en-Royans (Drôme) [France]. Two ♀.
The MHNG collection contains one specimen in alcohol under this name. The identification labels have "Caves de St. Nazaire" and "♀ Caves de Saint-Nazaire-en-Royans" handwritten on them, and the specimen is a syntype. There are also some more recently captured specimens, not part of the type series, under the name *Carloniscus dollfusi*. The other syntype is presumably in the MNHN, where Dollfus' collection is now deposited.
Carloniscus dollfusi (Carl, 1908)

eremitus Carl, 1908b: 18-19, fig. 8 [*Trichoniscus*].
Grotte de Sirach [France]. One ♂ and one ♀.
No specimens found in the MHNG. The syntypes are presumably in the MNHN, where Dollfus' collection is now deposited.
Oritoniscus eremitus (Carl, 1908)

gibbosus Carl, 1908a: 152-155, 8 figs in text [*Leucocyphoniscus*].
Grotta Tre Buchi, Grotte del Tanone (Monte Generoso) [Switzerland]. Unspecified number of ♂ and ♀.
The MHNG collection contains 15 specimens in alcohol, in two vials, under this name. The species name label in the jar has "Tessin mérid." written on it, but both vials have "Grotta de Tanone" written on the labels in them, one giving the date as "6.IX.07". There is also a label stating that the specimens were identified as "types" by A. Vandel in 1964. Since no holotype was designated, all of the specimens are syntypes.
Calconiscellus gibbosus (Carl, 1908)

medius Carl, 1908b: 19-21, fig. 9 [*Trichoniscus*].
Grotte de Sirach [France]. Unspecified number of ♂ and ♀.
No specimens found in the MHNG. The syntypes are presumably in the MNHN, where Dollfus' collection is now deposited.
Spelaeonthes medius (Carl, 1908)

mexicanus Saussure, 1857: 307 [*Porcellio*].
Mexique. Unspecified series.
Saussure (1858: 480) gave the locality more precisely as "Cordova et dans les régions chaudes du Mexique". The MHNG collection has two card-mounted specimens under this name, the specimens having originally been directly pinned. There is a third card mount with a detached antenna and some legs. The species name label has "Amer. centr., M H de Sauss." handwritten on it. Both specimens have small printed labels "Cordova t.c." and are syntypes. Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

montesumae Saussure, 1857: 307-308 [*Porcellio*].
Mexique (terres froides). Unspecified series.
Saussure (1858: 480) used the orthography "montezumae", gave the locality as "Tusitlan, à neuf lieues de Perote, dans les terres froides du Mexique", but also mentioned a specimen from near Cordoba. The MHNG has three card-mounted specimens, which were originally directly pinned, under this name, using the spelling "montezumae". One has a small printed label "Mexico t.f.", the second has a small handwritten label "Perote" and the third a small printed label "Cordova t.c." The species name label in the box has "Mexique, M H de Saussure" handwritten on it, and at least the first two specimens are syntypes. Crustacea box 18.
A junior synonym of *Porcellio scaber* Latreille, 1804

poeyi Saussure, 1857: 307 [*Porcellio*].
Cuba. Unspecified series.
The MHNG collection has one card-mounted specimen under the name "mexicanus (Poeyi Sss.)". The species name label has "Amer. centr., M H de Sauss." handwritten on it, and the specimen has a small printed label "Cuba". This specimen is a syntype. Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

propinquus Carl, 1908b: 15-17, fig. 7 [*Trichoniscus*].
Grotte les Demoiselles (Viré, 1897), Nimes (Chobaut) [France]. More than one ♂ and ♀.
The MHNG collection contains two specimens in alcohol, in one vial, under this name. Both identification labels in the vial have the locality "Grotte les Desmoiselles" handwritten on them, indicating that the specimens are syntypes. The other syntypes are presumably with the Dollfus collection in the MNHN.
Phymatoniscus propinquus (Carl, 1908)

pruinosa Carl, 1908a: 161-163, figs 69-71, 77, 155 [*Philoscia*].
Graubünden: Silvaplana-Moloja, St Moritz, Pontestrina, Cassacia, Viscosoprano Promotogno-Soligo Castasegna, Bernina-pass, Puschlav, Mesocco-Pian San Giacomo; Tessin: Val Blegno von Aquarossa, Leventina Faido-Rossura Piotta; St Gallen: Teufen [Switzerland]. Unspecified number of ♂ and ♀.
Carl (1911: 38) considered this name to be a junior synonym of *Philoscia germanicus* Verhoeff, 1896. *Philoscia germanicus* is currently regarded as a junior synonym of *Lepidoniscus minutus* (C. Koch, 1838). There are no specimens in the MHNG collection under any of those names. While it seems unlikely that all the specimens from so many localities have been lost, no type specimens could be identified in the MHNG collection.
Lepidoniscus pruinosus (Carl, 1908)

rathkei transalpina Carl, 1908a: 175-176 [*Porcellio*].
Muzzano, Carabbia am Monte Salvatore, Maroggia-Rovio, Monte Bré [Switzerland]. More than one ♀, some with juveniles.
Three vials containing syntypes were located amongst the dry material of the Carl duplicate collection, each with the identification label "Porcellio Rathkei var. transalpina" and the locality labels "Lugano, Carabbia, 6.IX.05", "Lugano – Muzzano, 3.9.05, Wald.Moos" and "Maroggia-Rovio 7.9.05." These specimens will be transferred to alcohol and placed in the main collection. This taxon is not listed in Schmalfuss (2003).
A junior synonym of *Trachelipus rathkii* (Brandt, 1833)

roseus nanus Carl, 1908a: 140-141, figs 8, 10 [*Trichoniscus*].
Frauenfeld, 12.x. Garten unter Brettern und Steinen, St. Gallen-Teufen, 9.x [Switzerland]. Unspecified number of ♂ and ♀.
Among the specimens in alcohol placed in the MHNG collection under the name *T. alpinus subterraneus* Carl, two vials (six specimens) were found with data labels "Fraunfeld 12.x.05, Garten unter Brettern und Steinen and "St. Gallen, Teufen, 9.x.05" and the identification "Trichoniscus roseus var." These are obviously the syntypes of Carl's subspecies because these localities were not mentioned by Carl for *T. subterraneus* and so the vials have now been moved to a separate jar. The name was placed in synonymy with *T. carynthiacus* Verhoeff by Carl (1911: 28), itself a junior synonym of *A. roseus* (C. Koch). *T. roseus nanus* is not listed in Schmalfuss (2003), but was included as a synonym of *A. roseus* by Vandel (1960).
A junior synonym of *Androniscus roseus* (C. Koch, 1838)

roseus subterraneus Carl, 1906: 606-607 [*Trichoniscus*].
Grotten von Osteino, dell'Alabastro, del Mago, Tre buchi, Tonane; Grotte in Val Tazzino bei Lugano [Switzerland]. Unspecified sereis (only ♂ mentioned explicitly).

Among the specimens in alcohol placed in the MHNG collection under the name *T. alpinus subterraneus* Carl were two vials containing syntypes. These have labels reading "Grotta bi Val Tazzino bei Lugano, ♂" (one specimen) and "Grotta del Mago bei Mendrusio, 5.ix.05, ♀" (three specimens). These have now been moved to a separate jar. The other vials all have labels giving localities listed under *T. roseus* by Carl (1908a, 1911) rather than in the original description of *T. roseus subterraneus*. These labels have the identification *T. roseus* Koch written on them, and the specimens are not syntypes.
Androniscus subterraneus (Carl, 1906)

sumichrasti Saussure, 1857: 307 [*Porcellio*].
Cuba. Unspecified series.
The MHNG has one card-mounted specimen under the name "cotillae (Sumichrasti Sss.)". The specimen was originally directly pinned, and has a small printed label reading "Cuba" and a handwritten label "51". The species name label in the box has "Cuba, M H de Saussure" handwritten on it, and the specimen is a syntype. Crustacea box 18.
A junior synonym of *Porcellio laevis* (Latreille, 1804)

virei Carl, 1908b: 220-221, fig. 5 [*Trichoniscus*].
Grottes de Tharaux, Grottes de Padirac (Dr Viré), Tinodule de la Vayssière, Grottes inférieures d'Avejan (Dr Viré), Baumes-Chaudes (Dr Viré) [France]. Two ♂ and many ♀.
The MHNG collection contains four specimens in alcohol under this name. The vial contains a data label "Grotte de Tharaux, Gard, 2.viii.1903", two identification labels with "Grotte de Tharaux, France" and "Grottes de Tharaux" written on them and an identification label "Trich. Virei Carl". These specimens are syntypes. The other syntypes are presumably in the MNHN, where Dolfuss' collection is now deposited.
Oritoniscus virei (Carl, 1908)

vividus montanus Carl, 1908a: 141-143, figs 22-42, 157 [*Trichoniscus*].
St. Gallen-Teufen, Teufen-Gais, Frauenfeld, Zürichberg, Laubwald, Zürich, Genf, Bern [Switzerland]. Many ♂ and ♀.
The MHNG collection has more than 50 specimens in alcohol, in seven tubes, under the name *T. montanus*. All of the tubes have data labels corresponding to localities mentioned in the original description and most also have dates in [19]05 on the labels. These specimens are syntypes. This taxon was raised to species rank by Carl (1911: 23).
A junior synonym of *Hyloniscus riparius* (C. Koch, 1838)

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REFERENCES

Carl J. 1904. Materialien zur Höhlenfauna der Krim. I Aufsatz. Neue Höhlencrustaceen. *Zoologischer Anzeiger* 28: 322-329.
Carl J. 1906. Beitrag zur Höhlenfauna der Insubrischen Region. *Revue suisse de Zoologie* 14: 601-615.
Carl J. 1908a. Monographie der schweizerischen Isopoden. *Neue Denkschriften der Schweizerischen Naturforschenden Gesellschaft* 42: 106-242, plates 1-6.
Carl J. 1908b. Etude sur les Trichoniscides de la collection de M. A Dollfus. *Feuille des jeunes naturalistes* 38: 169-172, 193-197, 220-223; 39: 15-21.
Carl J. 1911. Isopodes. *Catalogue des Invertébrés de la Suisse* 4: i-vi, 1-68.
Hollier A., Hollier J. 2013. A re-evaluation of the nineteenth-century naturalist Henri de Saussure. *Archives of Natural History* 40: 302-319.
Saussure H. de 1857. Diagnoses de quelques Crustacés nouveaux des Antilles et du Mexique. *Revue et magasin de zoologie pure et appliquée* 9: 304-308, 501-505.
Saussure H. de 1858. Mémoire sur divers crustacés nouveaux du Mexique et des Antilles. *Mémoires de la Société de physique et d'histoire naturelle de Genève* 14: 417-490, plates 1-6.
Schmalfuss H. 2003. World catalog of terrestrial isopods (Isopoda: Oniscidea). *Stuttgarter Beiträge zur Naturkunde* Serie A (Biologie) 654: 1-341.
Vandel A. 1960. Faune de France 64. Isopodes terrestres (première partie). *Fédération française des sociétés de sciences naturelles, Paris*. 416 pp.

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A European discovery: *Kalliste pavonum* gen. nov., sp. nov., the smallest phalangiid species known to date (Arachnida: Opiliones: Phalangiidae)

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Abstract: *Kalliste pavonum* is described as a new genus and new species of harvestmen based on males and females from the mountains of the island of Corsica, France. The new genus is characterized by male genitalia (massive truncus penis without distinct base, with extended penial muscle, dorsal subapical triangular tooth on stylus), pro-lateral apophyses on pedipalpal femur (female only), patella and tibia, two denticles with filiform apex on ventral side of palpal claw, large ocularium and minute body size. Superficially, the new species appears to be related to European genera with armed pedipalps, both together forming a basked-like structure, as found in *Rilaena*, *Megabunus*, *Metaplatybunus, Lophopilio* and *Platybunus*. However, they all differ from *Kalliste* gen. nov. by male genitalic characters and details of palpal armament. Apparently, *Platybunus* is the least closely related of these genera. *Kalliste* seems to be a rather isolated genus and species without close relatives within the West Palaearctic phalangiid assemblage.

Keywords: Taxonomy - relationships - genital morphology - new genus - new species - endemics - Corsica - France.

INTRODUCTION

During the last decades, very few new genera were established for newly detected and previously undescribed harvestmen species in Europe. Most spectacular was the discovery of a minute, short-range nemastomatid species in the Italian south-western Alps, which was named *Saccarella schilleri* Schönhofer & Martens, 2012. Here I establish another new genus for a recently recognized minute species of Phalangiidae from the island of Corsica, France. It probably escaped detection due to its small size and rather pale coloration, which resembles that of juveniles of co-occurring phalangiids.

MATERIAL AND METHODS

Original line drawings were produced using a camera lucida attached to a Carl Zeiss research microscope. Measurements were taken by means of a micrometer disc attached to a Leitz stereomicroscope. Measurements of the penis were taken from the original drawings. All measurements are given in mm.

In a strict morphological sense, in the Phalangiidae the glans of the penis is always bent to the dorsal side. Consequently, the upper side of the stylus (on the left side in Figs 19 and 21 and 23-24) is ventral; the stylus tooth on the opposite side is on the dorsal side.

Abbreviations of morphological terms:

Apo	apophysis
Cx	coxa
do	dorsal
Fe	femur
la	lateral
Mt	metatarsus
Op gen	operculum genitale
Pt	patella
Rec sem	receptaculum seminis
Ta	tarsus
Ti	tibia
Tr	trochanter
Tu oc	tuber oculorum, ocularium
ve	ventral

Museum acronyms:

CJM	Working collection of J. Martens, Mainz, Germany
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

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TAXONOMIC PART

Phalangiidae Latreille, 1802
Phalangiinae Latreille, 1802
***Kalliste* gen. nov.**

Type species: *Kalliste pavonum* sp. nov. (by original designation).

Diagnosis: Characterized by male genital morphology: truncus penis stout and massive, penial muscle much extended over more than proximal half of truncus. A subapical triangular tooth on lower (dorsal) side of penial stylus. Pedipalpal claw ventrally equipped with two thin proximal filiform denticles on a broader base. Strong and stout pedipalps with pro-lateral apophyses on femur (in female only), patella and tibia (in both sexes). Large elevated tuber oculorum occupying more than half of prosoma length. Small body size (1.8-2.0 mm in males, 1.9-2.6 mm in females).

Distribution: The single species of the new genus is known from two high-altitude localities in the mountains of central Corsica, France.

Name: Kalliste (τῇ καλλίστῃ) is one of the historical names of Corsica, used in times when the island was colonized by Greeks. It denominates the feminine superlative of kalós (καλός), "the most beautiful". The gender is feminine.

Relationships: See Discussion.

***Kalliste pavonum* sp. nov.**
Figs 1-27

Holotype: SMF; male; France, Corsica, Département Haute-Corse, Col de Verde, 1200 m; J. and B. Martens; leg. 26.8.2012.

Paratypes: CJM 3373; 2 males; France, Corsica, Département Haute-Corse, Col de Verde, 42°01'N, 9°11'E, 1280 m; B. Schröter [later B. Pfau] & K. Pfau; leg. 9.1982. – CJM 7255; 1 female; France, Corsica, Département Haute-Corse, Col de Vizzavona, 42°06'N, 9°06'E, 1000-1200 m; J. and B. Martens; leg. 8.9.2012. – MHNG; 1 male; France, Corsica, Département Haute-Corse, Col de Vizzavona, 42°06'N, 9°06'E, 1000-1200 m; J. and B. Martens; leg. 8.9.2012. – CJM 7267; 1 female; France, Corsica, Col de Verde, 1200 m; J. and B. Martens; leg. 26.8.2012.

Additional non-type material examined: CJM 7780; 2 juveniles; France, Corsica, Col de Vizzavona, 1000-1200 m; J. and B. Martens; leg. 29.8.2012 and 11.9.2012. – CJM 7781; 1 juvenile; France, Corsica, Col de Verde, 1200 m; J. and B. Martens; leg. 26.8.2012.

Diagnosis: At present, the diagnosis of genus *Kalliste* gen. nov. applies.

Remarks: It is noteworthy that *Kalliste pavonum* sp. nov. represents the smallest phalangiid species known to date. Tsurusaki (2007) mentions 2.2 mm as the minimum size for species of this family; *K. pavonum* sp. nov. is below that limit (see Measurements).

Name: *Kalliste pavonum* sp. nov. honors Beate and Klaus Pfau, distinctive zoologists who first provided specimens of this unusual species and put the material at my disposal. Pfau in Latin is "pavo", peafowl in English, "pavonum" is the plural genitive case referring to both collectors.

Description: MALE: *Body, dorsal side* (Figs 1, 5-6): Small, roundish, dorsal side without marked armament of granules, "hooks" or strong setae; only on 2nd thoracal segment with a loose row of low denticles (and a few setae), latero-distal and lateral rim of prosoma with small spiny protuberances.

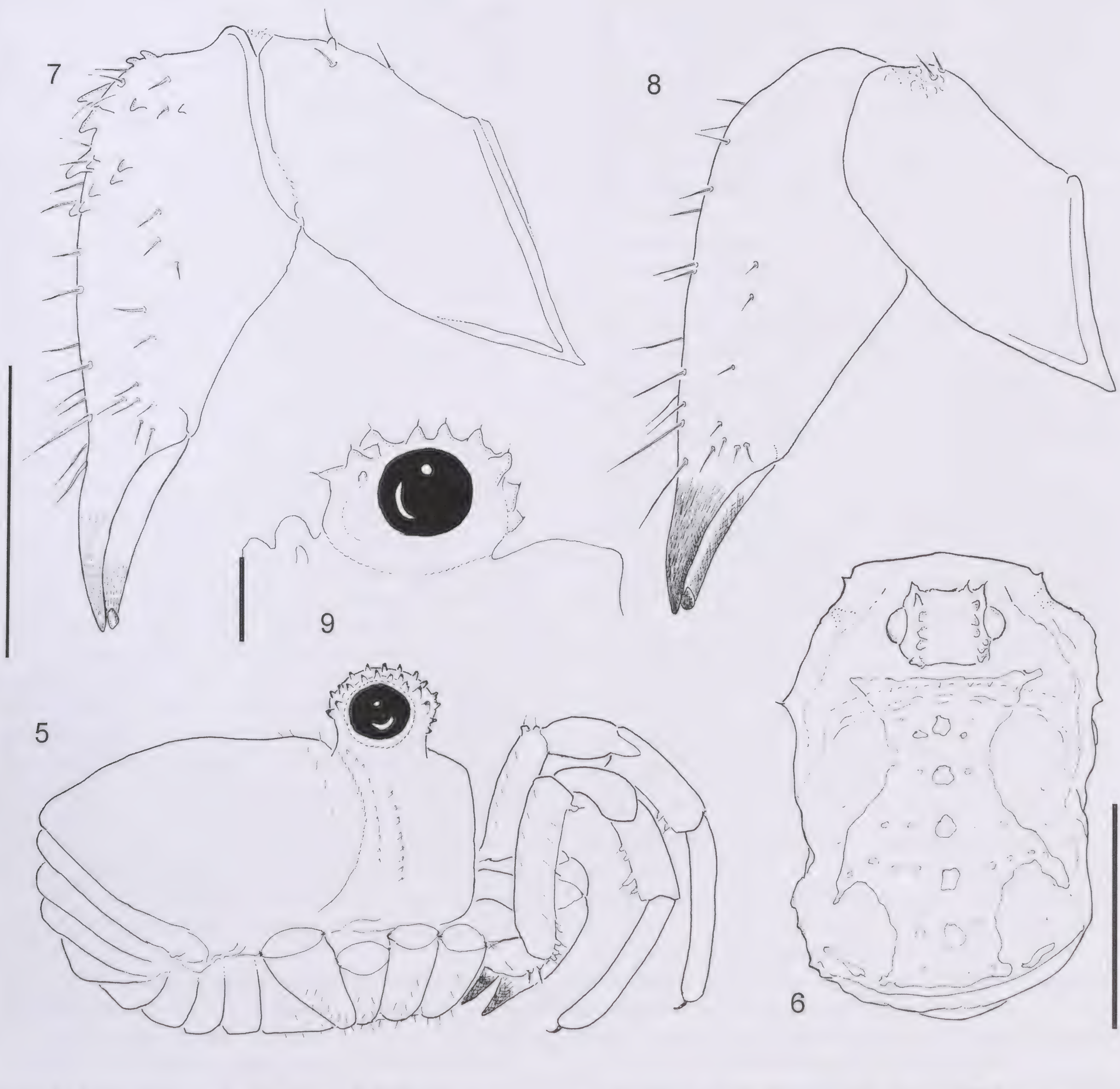
Figs 1-4. *Kalliste pavonum* gen. sp. nov. (1) Body of male holotype in dorsal view. (2) Same in ventral view. (3) Body of female paratype in dorsal view. (4) Same in ventral view. Scale: 0.5 mm.

Colour pattern (Figs 1, 6): Fully grown adults with shiny silvery ground colour and marked saddle pattern extending over dorsal thoracal segments and opisthosoma, broadest on metapeltidium, narrowest on opithosomal segment I, from there broadening to rear rim of segment II, then irregularly tapering toward segments III, IV and V of opisthosoma, causing a brownish appearance. Irregular rows of few light spots of different sizes across metapeltidium and opisthosomal segments, ocularium light silvery, large eyes black.

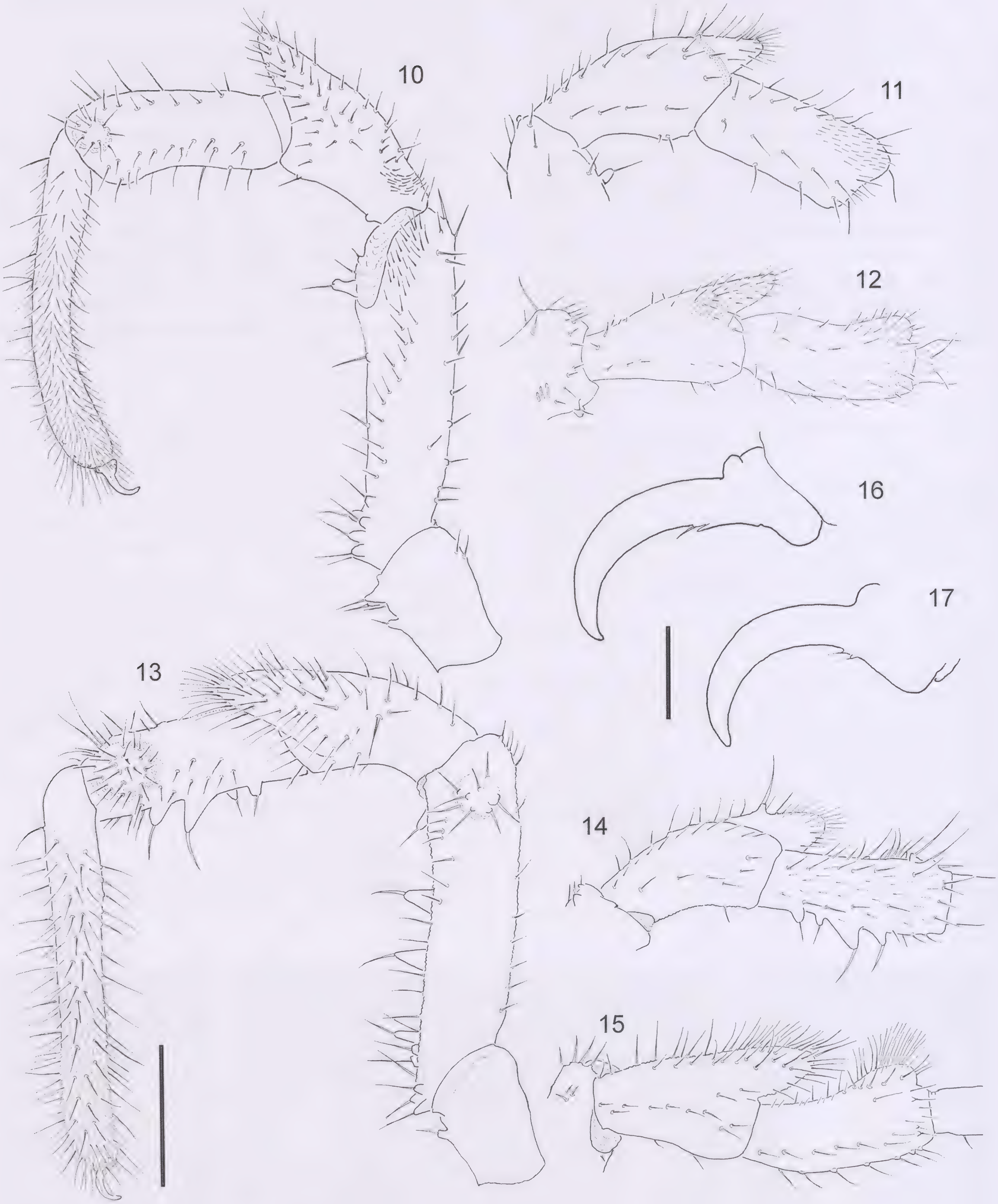
Tuber oculorum (Figs 1, 5-6, 9): Large (in comparison with other phalangiids), shiny, situated near posterior edge of prosoma, set back from anterior end of prosoma by about half of its length, dorso-laterally armed with two irregular rows of about 10-12 stout denticles, each one carrying a short seta.

Body, ventral side (Fig. 2): Cx with minute dark distal spot, otherwise like Op gen whitish with a yellow touch; free opisthosomal segments laterally light brown, medially with an irregular white stripe. Body unarmed except for few dark setae scattered on Cx and Op gen, shorter and hardly recognizable setae on opisthosomal segments.

Legs: Generally light to translucent, with broad, light brown, ring-shaped markings on Fe, Pt, Ti and Mt; size normal (in comparison with other phalangiids), with five sharply delimited longitudinal rows of minute, black, closely spaced setae accentuating the pentagonal cross



Figs 5-9. *Kalliste pavonum* gen. sp. nov. (5) Body of male holotype with chelicerae and pedipalps in lateral view. (6) Same (without chelicerae and pedipalps) in dorsal view. (7) Male chelicera in retro-lateral view. (8) Female chelicera in same view. (9) Male tuber oculorum in lateral view. Scales: 1.0 mm (Figs 5-6); 0.3 mm (Figs 7-8); 0.25 mm (Fig. 9).



Figs 10-17. *Kalliste pavonum* gen. sp. nov. (10-12) Male pedipalp in pro-lateral (10), retro-lateral (11) and dorsal view (12); patella and tibia only (11-12). (13-15) Female pedipalp in pro-lateral (13), retro-lateral (14) and dorsal view (15); patella and tibia only (14-15). (16-17) Palpal claws of male (16) and female (17), both from Col de Verde, lateral view. Scales: 0.3 mm (Figs 10-15); 0.03 mm (Figs 16-17).

section of Pt and Ti, less so of Fe; Mt and Ta with a rounded cross section; longest setae on tarsal articles; no denticles present on legs.

Pedipalp (Figs 10-12, 16): Translucent shiny, raptorial-clamp-type (by combination of both pedipalps) with strong equipment of Apo on Pt and Ti, massive spines on Fe and Ti ventrally, sexually dimorphic (see below). All articles stout and massive; Tr with few denticles and setae ventrally. Fe slightly bent ventrad, strong setae dorsally, pro-laterally and ventrally, on ventral side setae placed on blunt spines proximally and distally; a field of hairs (setae or microtrichia) present pro-laterally near distal end of Fe, at same position as knob-like Apo of female (see below). Pt large, with a prominent, pointed pro-lateral Apo directed slightly dorsad and distad, covered with strong setae; minute strong setae forming a curved field distally on pro-lateral side of Fe. Ti strong, slightly curved downwards, distinct knob-like pro-lateral Apo at distal end of article covered with few strong setae, longer setae present on dorsal and ventral side of Ti. Ta slender, curved ventrad, most slender in mid-part, tapering distally and proximally, covered all round with setae of different lengths, long and fine setae at distal end around the claw, minute trichomes interspersed. No ventral row (or band) of dark, sclerotized, point-like structures (as present in many species of various Phalangiinae genera). Claw (Fig. 16) well developed, on inner (ventral) side two fine, filiform denticles with a slightly broadened base (not a comb-like row of denticles like in Sclerosomatidae or *Dentizacheus* Rambla, 1956), situated in proximal half.

Chelicera (Fig. 7): Stout, 1st article short, with few denticles dorsally, 2nd article comparatively large, with several strong denticles at the proximal knee and on pro-lateral side, scattered setae frontally, pro- and retro-laterally; setae largest close to insertion of movable finger.

Penis morphology (Figs 18-26): Truncus penis (Figs 18-22) stout, enlarged base (in do/ve views) comprising about three fifth of whole truncus and containing penial muscle. Truncus from its base towards glans first slightly broadened for a short section, then slightly tapering and continuing more or less parallel-sided and slightly widening towards glans (in ve/do views). Base in la view (Figs 20, 22) much slenderer, less abruptly merging into distal part of truncus. Glans (Figs 23-24): In la view upper edge (i.e. ventral side) slightly concave, lower edge strongly bulging; two pairs of short setae in distal third of glans; in ve view strongly constricted at about mid-length. Stylus (Figs 25-26) strong and relatively long, with a broad triangular tooth sub-distally on lower (i.e. dorsal) side.

FEMALE (Figs 3-4, 8, 13-15, 17, 27): Similar to male, Tu oc situated even closer to prosoma frontal rim, shiny and armed as in male.

Coloration and dorsal saddle markings: As in male, segments VI and VII silvery white, ventral side as in male, ovipositor visible through translucent cuticle of Op gen.

Chelicera (Fig. 8): Proportions as in male, no denticles on 2nd article.

Pedipalp (Figs 13-15, 17): Similar to male but with spines, setae and Apo more strongly developed (i.e. the normal phalangiid condition). Fe with long setae and several strong tubercles topped by a seta each spread all over ventral side, distally on pro-lateral side a knob-like Apo covered with few strong setae. Pt with Apo like in male but more pronounced, distally slightly rounded. Ti massive, ventrally with four spines of different sizes topped by a long seta each, pro-laterally at distal end a large knob-like Apo covering nearly entire depth of article (in pro-lateral view, Fig. 13), long setae mainly in distal part of article. Ta being the longest article, straight, slightly tapering towards distal end, covered by long setae all over, longest setae nearly reaching depth of article (in la view), in addition a dense coat of microtrichia. Claw (Fig. 17) generally similar to that of male, lower (concave) side with two small denticles, each carrying a filiform apex, about twice as long as base, located in proximal half of claw.

Legs: Proportions similar to those of male; slightly less strong, black, closely spaced setae present; Pt less pentagonal but more rounded in cross section.

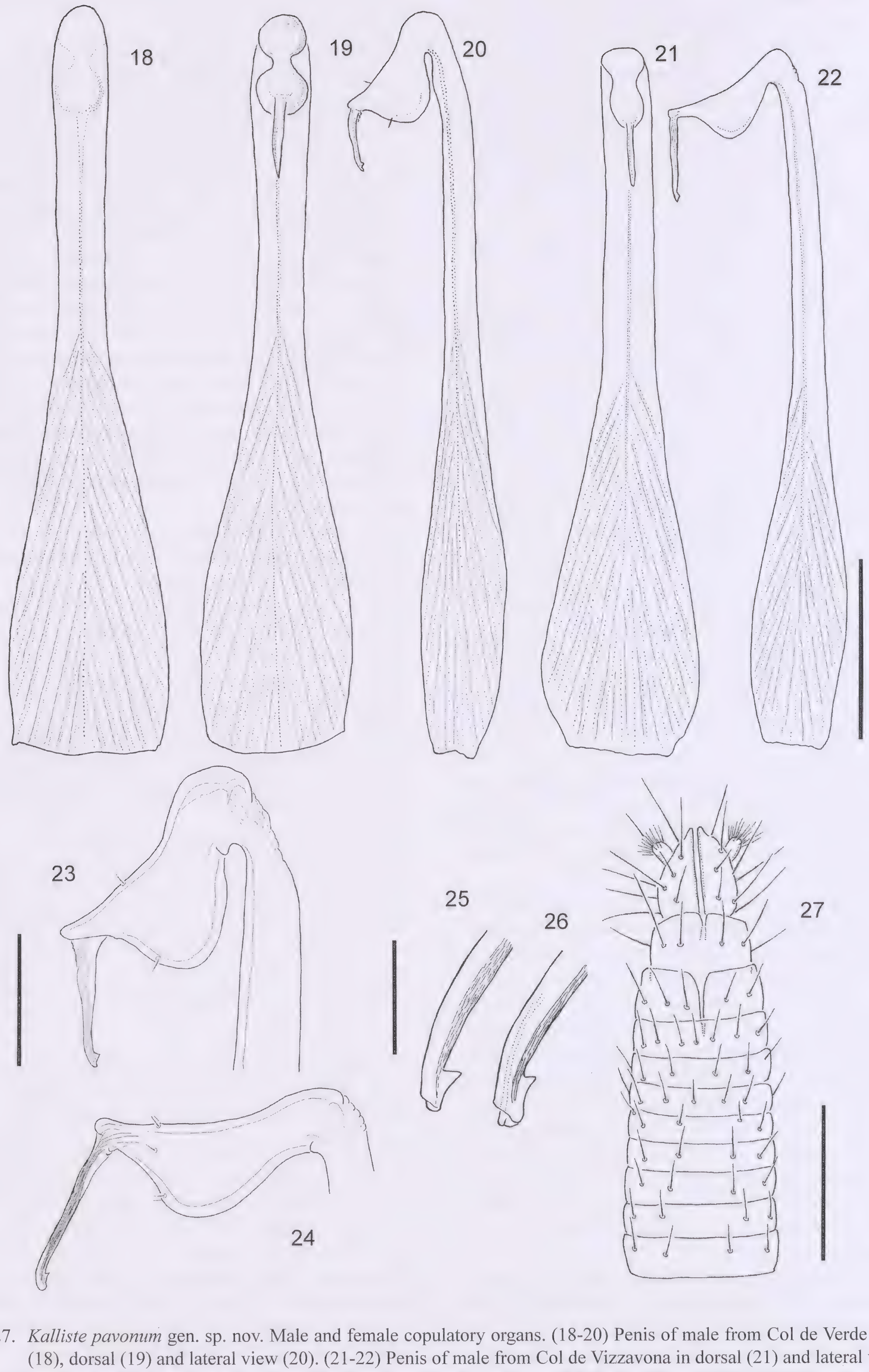
Ovipositor morphology (Fig. 27): Two complete distal segment rings broader than proximal ones, three distal rings more or less distinctly split (last one completely split, second last one split only distally, third last one completely split). Long setae on two distal rings, shorter ones on proximal rings. Rec sem not recognizable. Disto-lateral bulbs on last segment longish, distally covered by long fine setae forming a compound sensillum (Hoheisel & Martens, 1990).

Measurements: Body length of males 1.8-2.0 (n=4), of females: 1.9-2.6 (n=3). Leg II length of male (holotype), in parantheses of female paratype: Fe 2.7 (2.2), Pt 0.7 (0.6), Ti 2.3 (2.0), Mt 1.9 (1.4), Ta 5.3 (4.3). Pedipalp length of male, in parentheses of female: Tr 0.25 (0.25) Fe 0.6 (0.6), Pt 0.35 (0.4), Ti 0.4 (0.4), Ta 0.6 (0.8). Penis length of holotype and of one male paratype (n=2): 0.9, 1.0.

Variation: Shape of glans and length of stylus of glans vary remarkably (Figs 23-26). Due to sparse material, detailed information is presently not available.

Distribution, habitat and phenology: According to present knowledge, *K. pavonum* sp. nov. is confined to the central mountainous parts of the island of Corsica (France) and until now only known from two high-altitude passes, Col de Verde and Col de Vizzavona. These are in easy reach by car on good roads, about 35 km east of Aléria on the eastern coast. The two localities are separated from each other by approximately 12 km linear distance.

The specimens were found on the ground, under stones and dead wood, in forests dominated by beech (*Fagus sylvatica*). Present records lie between 1000-1200 m.



Figs 18-27. *Kalliste pavonum* gen. sp. nov. Male and female copulatory organs. (18-20) Penis of male from Col de Verde in ventral (18), dorsal (19) and lateral view (20). (21-22) Penis of male from Col de Vizzavona in dorsal (21) and lateral view (22). (23-24) Stylus, glans and distal part of truncus penis in lateral view (23: Col de Verde, 24: Col de Vizzavona). (25-26) Distal part of stylus in lateral view (25: Col de Verde, 26: Col de Vizzavona). (27) Distal part of ovipositor in ventral view. Scales: 0.3 mm (Figs 18-22); 0.05 mm (Figs 23-24); 0.025 mm (Figs 25-26); 0.2 mm (Fig. 27).

Maturity time is August and September and may extend at least to the onset of frost; juveniles were also collected in August and September (see Material). Because of its small size and light colour, specimens of this species are easily overlooked among juveniles of other species to which adults of *K. pavonum* sp. nov. look similar.

DISCUSSION

New genera records: During the last decades, new genera of harvestmen were rarely established for newly detected and previously undescribed species in Europe. None of them has been evaluated in a broader context using also molecular genetic analyses; all of them have to be regarded as hypotheses. Most prominent are *Lola insularis* Kratochvíl, 1937 (cavernicolous; Phalangodidae; Croatia), *Paralola buresi* Kratochvíl, 1958 (cavernicolous; Travuniidae; Bulgaria), *Tranteeva paradoxa* Kratochvíl, 1958 (cavernicolous; Sironidae; Bulgaria), *Odontosiro lusitanicus* Juberthie, 1961, *Paramiopsalis ramulosus* Juberthie, 1962 (both surface-dwelling, in litter, Sironidae; Portugal), *Rilaena balcanica* Šilhavý, 1965 (surface-dwelling; Phalangiidae; Bulgaria), *Anarthrotarsus martensi* Šilhavý, 1967 (surface-dwelling, in litter, Trogulidae; Greece), *Ausobskya athos* Martens, 1972 (surface-dwelling, in litter; Phalangodidae; Greece), *Iberosiro distylos* de Bivort & Giribet, 2004 (cavernicolous; Sironidae; Portugal) and *Saccarella schilleri* Schönhofer & Martens, 2012 (surface-dwelling, in litter; Nemastomatidae; Italian south-western Alps). Thus, the present discovery of a surface-dwelling, non-cavernicolous, minute phalangiid species for which a new genus needs to be established comes quite unexpected. The new species lives in remote mountainous areas of Corsica, an island which is known for a number of endemics in various animals groups, including vertebrates, like the famous Corsican nuthatch (*Sitta whiteheadi*). Several endemic opilionid species were described from this island, among them *Parasiro corsicus* (Simon, 1872), *P. minor* Juberthie, 1958, *Trogulus aquaticus* Simon, 1879, *Anelasmocephalus pusillus* Simon, 1879, *Nelima ponticoides* Martens, 1969 and *Dicranopalpus insignipalpis* Simon, 1879. One undescribed species each of the genera *Mitostoma* Roewer, 1951 and *Lacinius* Thorell, 1876, also from Corsica, await formal description. Presumably, *Kalliste pavonum* sp. nov. will turn out to be another insular endemic, and presently its relationships can only be discussed with reservations. Opilionid species assemblage of the neighbouring island Sardinia, larger than Corsica but less mountainous, differs markedly. Marcellino (1982) provided a comparative overview which in the meantime is somewhat outdated.

Genus level systematics: *Kalliste* nov. gen. belongs to a set of phalangiid genera which has the pedipalpal articles patella and tibia armed with a strong disto-prolateral apophysis each. Ventrally, the pedipalp articles (namely femur, patella and tibia) of these species are often armed with strong seta-bearing tubercles, but numbers and arrangement vary. This armament forms an effective prey-catching basket, the clamp type of pedipalps, in *Kalliste* better called a "raptorial clamp type" (Wolff *et al.*, 2016: fig. 12). Within the European fauna, genera possessing this set of characters belong to *Rilaena* Šilhavý, 1965, *Megabunus* Meade, 1885, *Metaplatybunus* Roewer, 1911, *Lophopilio* Hadži, 1931 and *Platybunus* C.L. Koch, 1839. This congruence of characters may indicate close relationships but convergent development seems more plausible because the similarities in pedipalp morphology seem to be superficial and may even be plesiomorphic for a lineage within the Palangiidae.

Rilaena is a highly heterogeneous genus to which, after its erection by Šilhavý (1965), a number of mainly Near East and Central Asian species was added. Apparently, *Rilaena* does not comprise a monophyletic entity but contains a number of superficially similar but not closely related species (personal observation).

Megabunus is a peculiar genus of rock-face-dwelling species of the Alps (plus two additional species from western Europe and former Yugoslavia) to which recently three alpine species were added following a molecular genetic analysis (Wachter *et al.*, 2015). With respect to *Kalliste* nov. gen. it exhibits similar features in genital morphology, i.e. rather compact form of truncus penis, but details markedly differ, i.e. extent of penial muscle, form of glans and size. Also armament and shape of the ocularium are quite dissimilar.

Metaplatybunus has its main diversity in the Mediterranean and also includes a number of species from the Balkan peninsula, Turkey and the near East. Most of its species are not revised and properly described yet, additional ones await formal description. Generally, *Metaplatybunus* comprises large species with strong denticles and spines on legs and pedipalps and with a heavily armed large, broad ocularium. Presumably also the species currently included in this genus will turn out to be a quite heterogeneous assemblage once molecular genetic analyses are applied.

Lophopilio stands out by a strong and heavy truncus penis which appears triangular in cross section and by a peculiar armament of its ocularium. This is a rather isolated monotypic genus.

Platybunus is not a member of this assemblage because of its distinctly different male genital morphology, especially the extremely slender truncus and glans of its penis, and because of the different shapes of body and ocularium. Staręga (1976) even erected a separate subfamily, Platybuninae Staręga, 1976, to highlight these differences. He also added *Lophopilio* to Platybuninae, its sole species being quite dissimilar to *Platybunus* species.

In addition, all the males and often also females of the

species of the beforementioned genera have in common a rounded, knob-like apophysis in the distal part of the pro-lateral side of the femur; this character is absent in *Kalliste pavonum* sp. nov. males.

Character development: Most probably the raptorial clamp-shaped pedipalps of these phalangiid genera developed independently several times as a most effective basket-like device for capturing and further manipulating prey prior to intake. This hypothesis is supported by the fact that many interior (copulatory organs) and exterior (pedipalps, ocularium, body form and size, ecology) characters of the species of these genera differ in many details, indicating separate evolutionary units.

Also in other families of Eupnoi, e.g. in the Sclerosomatidae, a family related to Phalangiidae, basked-like structures developed on the pedipalps, but this happened rarely. Wolff *et al.* (2016) illustrated an unnamed juvenile sclerosomatid specimen with distinct patellar and tibial apophysis, and Martens (1973, 1982, 1987) presented several sclerosomatid species of various genera from Nepal bearing such apophyses at least on the palpal patella. As sclerosomatids generally do not possess clamp-type pedipalps with seta-bearing denticles, this may be another indication of parallel evolution of this pedipalp type in Eupnoi.

Another characteristic feature which may prove useful to track relationships in Phalangiidae is the muscle portion of the truncus penis. This muscle, which moves the glans upward into a distal position by means of a muscle-tendon-system (Martens, 1976), is always located in the proximal part of the truncus. However, extent of the muscle and shape of the truncus part harbouring the muscle largely differ between genera, less so between species of single genera. Muscle size is able to influence penis shape, *vice versa* probably also penis shape can influence the extent of the muscle. Generally, truncus penis shape in phalangiids follows a simple pattern: from its base the truncus is tapering towards the glans insertion, the muscle is situated in the base, i.e. the largest, most voluminous part of the truncus. The possible degree of modification is limited; it varies from a largely unmodified truncus to one with a small, bulbous base which is well differentiated from the remainder of the truncus. An extended muscle with a short tendon and, as a morphological consequence, a vaguely enlarged (or undifferentiated) truncus base is generally regarded as plesiomorphic, whereas a shorter muscle, concentrated in a bulbous base and attached to a long tendon, as apomorphic. This assumption is supported by the fact that in molecular genetic analyses of Nemastomatidae, a dyspnoian family, the species of the genus *Mitostoma* Roewer, 1951, characterized by large extended muscles (in this family always two muscles are present) are sister to all other nemastomatid genera so far analysed. In contrast, a distinctly separated base with a small and compact penis muscle, as seen in *Paranemastoma* Redikorzev, 1936 and related genera, form a distantly related clade (Schönhofer & Martens, 2010). *Kalliste* gen. nov. exhibits a large, "heavy" penis with a muscle extending up to the distal part of the truncus, but slight variation in length occurs (two penes examined). In view of this truncus-muscle-ratio, a close relationship of *Kalliste* gen. nov. to any of the above mentioned phalangiid genera seems unlikely. On the other hand, genital morphological characters of *Kalliste* gen. nov. do not match those of any other European or Near Eastern genus, the species of which possess non-raptorial clamp-like pedipalps like in *Phalangium* Linnaeus, 1758 or *Eudasylobus* Roewer, 1911.

Two more characters attribute *Kalliste* gen. nov. an outstanding position within the Phalangiidae: a tooth on the glans stylus and filiform denticles on the palpal claw. A tooth at the stylus tip is known solely in *Phalangium opilio* Linnaeus, 1758, situated sub-distally on the ventral side. In *Kalliste* gen. nov. the hook is on the dorsal side. Šilhavý (1948, 1956) who meticulously illustrated details of glans and stylus of Central European Phalangiidae, found it only in this species.

The two filiform denticles on top of a broader base on the ventral (i.e. inner) side of the palpal claw in *Kalliste* gen. nov. are unique as well. Dentate palpal claws in Phalangiidae have been described in *Rilaena balcanica* Šilhavý, 1965 and *Dentizacheus tinerfensis* Rambla, 1956, but they differ in details. In *Kalliste* gen. nov. the denticles end in a long filiform apex, something not found in any phalangiid or sclerosomatid species. Šilhavý (1961) defined a whole subfamily, the Dentizacheinae, on the basis of strongly dentate palpal claws, which was never accepted as a valid taxon (Crawford, 1992). Staręga (1973) placed it in the synonymy of the Phalangiinae. With regard to the characters discussed above, *Kalliste* gen. nov. thus seems to be a rather isolated genus and species without close relatives within the West Palearctic opilionid assemblage.

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BIBLIOGRAPHIC REFERENCES

Crawford R.L. 1992. Catalogue of the genera and type species of the harvestman superfamily Phalangioidea (Arachnida). *Burke Museum contributions in anthropology and natural history* 8: 1-60.

de Bivort B. L., Giribet G. 2004. A new genus of cyphophthalmid from the Iberian Peninsula with a phylogenetic analysis of the Sironidae (Arachnida: Opiliones: Cyphophthalmi) and a SEM database of external morphology. *Invertebrate Systematics* 18: 7-52.

Hadži J. 1931. Opilioni Triglavskoga masiva (Die Opilionen des Triglavmassivs). *Prirodoslovne Razprave, Muzejsko Drustvo za Slovenijo* 1: 107-154.

Hoheisel U., Martens J. 1990. Die Sensillenfelder des Ovipositors von *Phalangium opilio* Linné (Arachnida: Opiliones: Phalangiidae). *Zoologische Jahrbücher für Anatomie der Tiere* 129: 63-79.

Juberthie C. 1958. Révision du genre *Parasiro* (Opilions, Sironidae) et description de *Parasiro minor* n. sp. *Bulletin du Muséum National d'Histoire Naturelle* (2e série) 30: 159-166.

Juberthie C. 1961. Etude des opilions cyphophthalmes (arachnides) du Portugal: description d'*Odontosiro lusitanicus* g. n., sp. n. *Bulletin du Muséum National d'Histoire Naturelle* (2e série) 33: 512-519.

Juberthie C. 1962. Etude des opilions cyphophthalmes Stylocellinae du Portugal. Description de *Paramiopsalis ramulosus* gen. n., sp. n. *Bulletin du Muséum National d'Histoire Naturelle* (2e série) 34: 267-275.

Koch C. L. 1839. Übersicht des Arachnidensystems, 2. *C.H. Zeh, Nürnberg*, 38 pp.

Kratochvíl J. 1937. *Lola insularis* nov. gen. nov spec. (Fam. Phalangodidae) a *Travunia* (?) *jandai* nov. spec. (Fam. Travuniidae), dva noví jeskynní sekáči z jihodalmatských ostrovů. *Folia entomologica* 1: 44-54.

Kratochvíl J. 1958. Höhlenweberknechte Bulgariens (Palpatores - Nemastomatidae). *Práce Brněnské základny Československé akademie věd* 30(12): 523-576.

Latreille P.-A. 1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. *Dufart, Paris* pp. 1-445.

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. *L. Salvius, Holmiae*, 824 pp.

Marcellino I. 1982. Opilioni di Sardegna (Arachnida, Opiliones). *Lavori della Società Italiana di Biogeographia* (N.S.) 9: 413-434.

Martens J. 1969. Mittel- und südeuropäische Arten der Gattung *Nelima* (Arachnida, Opiliones, Leiobunidae). *Senckenbergiana biologica* 50: 395-415.

Martens J. 1972. *Ausobskya athos*, der erste Krallenweberknecht aus Griechenland (Opiliones: Phalangodidae). Mit Bemerkungen zur Familien-Gliederung der europäischen Laniatores. *Senckenbergiana biologica* 53: 431-440.

Martens J. 1973. Opiliones aus dem Nepal-Himalaya. II. Phalangiidae und Sclerosomatidae (Arachnida). *Senckenbergiana biologica* 54: 181-217.

Martens J. 1976. Genitalmorphologie, System und Phylogenie der Weberknechte (Arachnida: Opiliones). *Entomologica Germanica* 3: 51-68.

Martens J. 1982. Opiliones aus dem Nepal-Himalaya. V. Gyantinae (Arachnida: Phalangiidae). *Senckenbergiana biologica* 62: 313-348.

Martens J. 1987. Opiliones aus dem Nepal-Himalaya. VI. Gagrellinae (Arachnida: Phalangiidae). *Courier Forschungs-Institut Senckenberg* 93: 87-202.

Meade R. H. 1885. Monograph on the British species of Phalangiidae or harvest-men. *The Annals and Magazine of Natural History including Zoology, Botany and Geology* (Ser. 2) 15(90): 393-416.

Rambla M. 1956. Nota sobre algunos Opiliones de la isla de Tenerife. *Publicaciones del Instituto de Biologia Aplicada* 22: 29-41.

Redikorzev V.V. 1936. Materialy k faune Opiliones SSSR. *Trudy zoologiceskogo Instituta, Akademija Nauk SSSR* 3: 33-57.

Roewer C.-F. 1911. Übersicht der Genera der Subfamilie der Phalangiini der Opiliones Palpatores nebst Beschreibungen einiger neuer Gattungen und Arten. *Archiv für Naturgeschichte* 77(suppl. 2): 1-106.

Roewer C.-F. 1951. Über Nemastomatiden. Weitere Weberknechte XVI. *Senckenbergiana* 32: 95-135.

Schönhofer A.L., Martens J. 2010. Hidden Mediterranean diversity: Assessing species taxa by molecular phylogeny within the opilionid family Trogulidae (Arachnida, Opiliones). *Molecular Phylogenetics and Evolution* 54: 59-75.

Schönhofer A.L., Martens J. 2012. The enigmatic Alpine opilionid *Saccarella schilleri* gen. n., sp. n. (Arachnida: Nemastomatidae) – isolated systematic placement inferred from comparative genital morphology. *Organisms, Diversity & Evolution* 12: 409-419.

Šilhavý V. 1948. Les Opilions de la steppe de serpentine près de la ville de Mohelno. *Acta publica Societatis pro cognitione et conservatione naturae in Moraviae Silesiaeque finibus. Mohelno. Collectio studiorum ad monumentum naturae prefaestantem cognoscendum* 8: 1-108.

Šilhavý V. 1956. Sekáči – Opilionidea, Fauna ČSR 7. Československé Akademie Věd, *Praha*, 272 pp.

Šilhavý, V. 1961. Die Grundsätze der modernen Weberknechttaxonomie und Revision des bisherigen Systems der Opilioniden. *XI. Internationaler Kongress für Entomologie Wien 1960. Verhandlungen* 1: 262-267.

Šilhavý V. 1965. Die Weberknechte der Unterordnung Eupnoi aus Bulgarien, zugleich eine Revision europäischer Gattungen der Unterfamilien Oligolophinae and Phalangiinae (Arachnoidea, Opilionidea). *Acta entomologica bohemoslovaca* 62: 369-406.

Šilhavý V. 1967. *Anarthrotarsus martensi*, ein neuer Weberknecht aus Griechenland. (Arach., Opiliones). *Senckenbergiana biologica* 48: 175-178.

Simon E. 1872. Notices sur les arachnides cavernicoles et hypogés et notice complémentaire. *Annales de la Société entomologique de France* (ser. 5) 2: 215-244.

Simon E. 1879. Les ordres des Chernetes, Scorpiones et Opiliones. *Les Arachnides de France* 7: 1-332.

Staręga W. 1973. Bemerkungen über einige westpaläarktische Weberknechte (Opiliones). *Annales Zoologici* 30: 361-373.

Staręga W. 1976. Opiliones, Kosarze (Arachnoidea). *Fauna Polski* 5: 1-197.

Thorell T. 1876. Sopra alcuni Opilioni (Phalangidea) d'Europa e dell'Asia occidentale, con un quadro dei generi europei di quest'Ordine. *Annali del Museo civico di storia naturale di Genova* 8: 452-508.

Tsurusaki N. 2007. Phalangiidae Latreille, 1802 (pp. 123-126). *In*: Pinto-da-Rocha R., Machado G., Giribet G. (eds). Harvestmen, the biology of Opiliones. *Harvard University Press, Cambridge*, 597 pp.

Wachter G.A., Muster C., Arthofer W., Raspotnig G., Föttinger P., Komposch C., Steiner F.M., Schlick-Steiner B.C. 2015. Taking the discovery approach in integrative taxonomy: decrypting a complex of narrow-endemic Alpine harvestmen (Opiliones: Phalangiidae: *Megabunus*). *Molecular Ecology* 24(4): 863-889.

Wolff J.O., Schönhofer A.L., Martens J., Wijnhoven H., Taylor C.K., Gorb S.N. 2016. The evolution of pedipalps and glandular hairs as predatory devices in harvestmen (Arachnida, Opiliones). *Zoological Journal of the Linnean Society* 177: 558-601.

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A revision of the Chilean Brachyglutini – Part 3. Revision of *Achilia* Reitter, 1890: *A. frontalis* species group (Coleoptera: Staphylinidae: Pselaphinae)

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Abstract: The *Achilia frontalis* species group (*sensu* Jeannel, 1962, 1964) of the species-rich genus *Achilia* Reitter, 1890 is revised. Of the thirteen taxa placed in this group of species, five names are here synonymised: *A. validicornis* Jeannel, 1962 = *A. excisa* (Schaufuss, 1880) (**syn. nov**.), *A. pseudovalidicornis* Franz, 1996 = *A. pachycera* Jeannel, 1963 (**syn. nov**.), *A. acicularis* Jeannel, 1962 = *A. testacea* Jeannel, 1962 (**syn. nov**.), *A. foveifrons* Jeannel, 1962 = *A. frontalis* Jeannel, 1962 (**syn. nov**.), and *A. validicorniformis* Franz, 1996 = *A. larvata* (Reitter, 1885) (**syn. nov**.). Lectotypes are designated for *A. excisa* and *A. validicornis*. The remaining eight species are redescribed, their main diagnostic features are illustrated, their distributions are detailed, and data available on habitat/collecting are summarised. Two new species – *Achilia trauco* **sp. nov.** and *Achilia fiura* **sp. nov.** – are also described and added to the group, while *A. longispina* Franz, 1996, is removed from it.

Keywords: Chile - taxonomy - new species - new synonyms - distribution.

INTRODUCTION

This article is the third contribution in a series dedicated to a taxonomic revision of Brachyglutini of temperate region of southern South America (Kurbatov & Sabella, 2015; Sabella *et al*., 2017). We here focus on the *Achilia frontalis* species group (*sensu* Jeannel, 1962 and 1964). The members are critically reexamined, and each species is redescribed, its synonymic framework and distribution are detailed, collecting data are summarised, and the new species *Achilia trauco* n. sp. and *Achilia fiura* n. sp. are described. The opportunity to maintain these species groups of *Achilia*, which are mainly based on male sexual dimorphism, as well as their possible phylogenetic relationships will be reassessed later. A key to identification of the species will also be provided only at the end of this series of contributions.

MATERIAL AND METHODS

This study is based on the examination of 2309 specimens.

The acronyms used in this study refer to the following collections (relevant curator/collection manager acknowledged in parenthesis):

DBUC Department of Biological, Geological and Environmental Sciences, University of Catania, Italy

FMNH Field Museum of Natural History, Chicago, U.S.A. (J. Boone)

MHNG Muséum d'histoire naturelle, Genève, Switzerland

MNHN Muséum national d'Histoire naturelle, Paris, France (T. Deuve and A. Taghavian)

MNHS Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta Donoso and Y. J. Sepulveda Guaico)

MSNG Museo Civico di Storia Naturale "G. Doria", Genova, Italy (R. Poggi)

NHMW Naturhistorische Museum, Wien, Austria (H. Schillhammer)

PHPC Private collection of Peter Hlavác, Prague, Czech Republic (P. Hlavác)

UNHC University of New Hampshire Arthropod Collection, Durham, NH, U.S.A. (D.S. Chandler)

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Under the sections "type material" or "additional material" the locality data are standardised, with indications of major administrative units (regions and provinces) and names of collectors. For the method of selection of the type materials see Sabella *et al.* (2017). The body length is measured from the anterior clypeal margin to the posterior margin of the last visible abdominal tergite. The length and width of body parts were measured between points of maximum extension, e.g. the head length is measured between the anterior clypeal margin and the posterior margin of the neck; the head width includes the eyes, the elytral length along the suture line, and the elytral width is the total width of the two elytra taken together. The abdominal tergites are numbered based on order of visibility. Morphological terminology follows that of Chandler (2001), except that the abdominal sternites are termed ventrites here, and that the sclerotised features of the dorsal plate of the aedeagus termed "dorsal strips" in Sabella *et al.* (2017) are termed "longitudinal struts" here.

TAXONOMY

Achilia frontalis species group

Jeannel (1962: 397, 408-409) distinguished the *A. validicornis* and *A. frontalis* groups by the number of elytral basal foveae (2 in the *A. validicornis* group and 3 in the *A. frontalis* group), and the shape of the copulatory pieces of the aedeagus (ramified in the *A. validicornis* group and not ramified in the *A. frontalis* group).
One year later he described *Achilia pachycera* as a new member of the *A. frontalis* group (Jeannel 1963: 363). However, shortly thereafter Jeannel (1964: 10) pointed out that *A. pachycera* was very similar to *A. validicornis,* and that the latter species belonged indeed to the *A. frontalis* group, implicitly sinking his *A. validicornis* group into the *A. frontalis* group. Consequently the species described later by Franz (1996: 116-117) in the *A. validicornis* group – i.e. *A. pseudovalidicornis*, *A. longispina* and *A. validicorniformis* – technically also belong to the *A. frontalis* group.
According to Jeannel (1962 and 1964) the species of the *A. frontalis* group are characterised by: 2 or 3 elytral basal foveae; basal striae of abdominal tergite I separate at most by 1/3 of tergal width; frons of male with a high and narrow median protuberance flanked by two more or less deep pits with the outer margin often toothed; antennomeres unmodified; copulatory pieces of the aedeagus thin and ramified, or not.
As defined the group currently includes: *A. acicularis* Jeannel, 1962, *A. auriculata* Jeannel, 1962, *A. caracolana* Jeannel, 1962, *A. excisa* (Schaufuss, 1880), *A. foveifrons* Jeannel, 1962, *A. frontalis* Jeannel, 1962, *A. longispina* Franz, 1996, *A. ovallensis* Jeannel, 1962, *A. pachycera* Jeannel, 1963, *A. pseudovalidicornis* Franz, 1996, *A. testacea* Jeannel, 1962, *A. validicornis* (Reitter, 1885), and *A. validicorniformis* Franz, 1996.
However, in addition all species, except *A. longispina*, share the following features: pubescence decumbent with long setae, uniform on entire body; head wider than long; surface of head smooth, shiny, with some punctures; frontal lobe with rounded apex; vertexal sulcus impressed; vertexal foveae shallow and broad (not visible in males of *A. excisa*, *A. pachycera*, *A. fiura* n. sp., *A. caracolana*, *A. frontalis*); eyes protruding; temples convex; pronotum wider than long; anterior portion of lateral margins of pronotum convergent, posterior portion subparallel and sinuate; pronotal disc slightly convex, smooth and shiny with some punctures; basal margin of pronotum bordered with row of contiguous shallow impressions; elytra together wider than long, with protruding humeri; elytral disc smooth, shiny, with punctures; presence of four basal foveae (two lateral foveae very close); sutural stria entire; discal stria extending to about elytral midlength; legs rather long; abdomen smooth, with some minute punctures; tergite I with short and sparse setal brush between basal striae.
In order to keep the text more concise, these features are not repeated in the descriptions below.

Achilia excisa (Schaufuss, 1880)

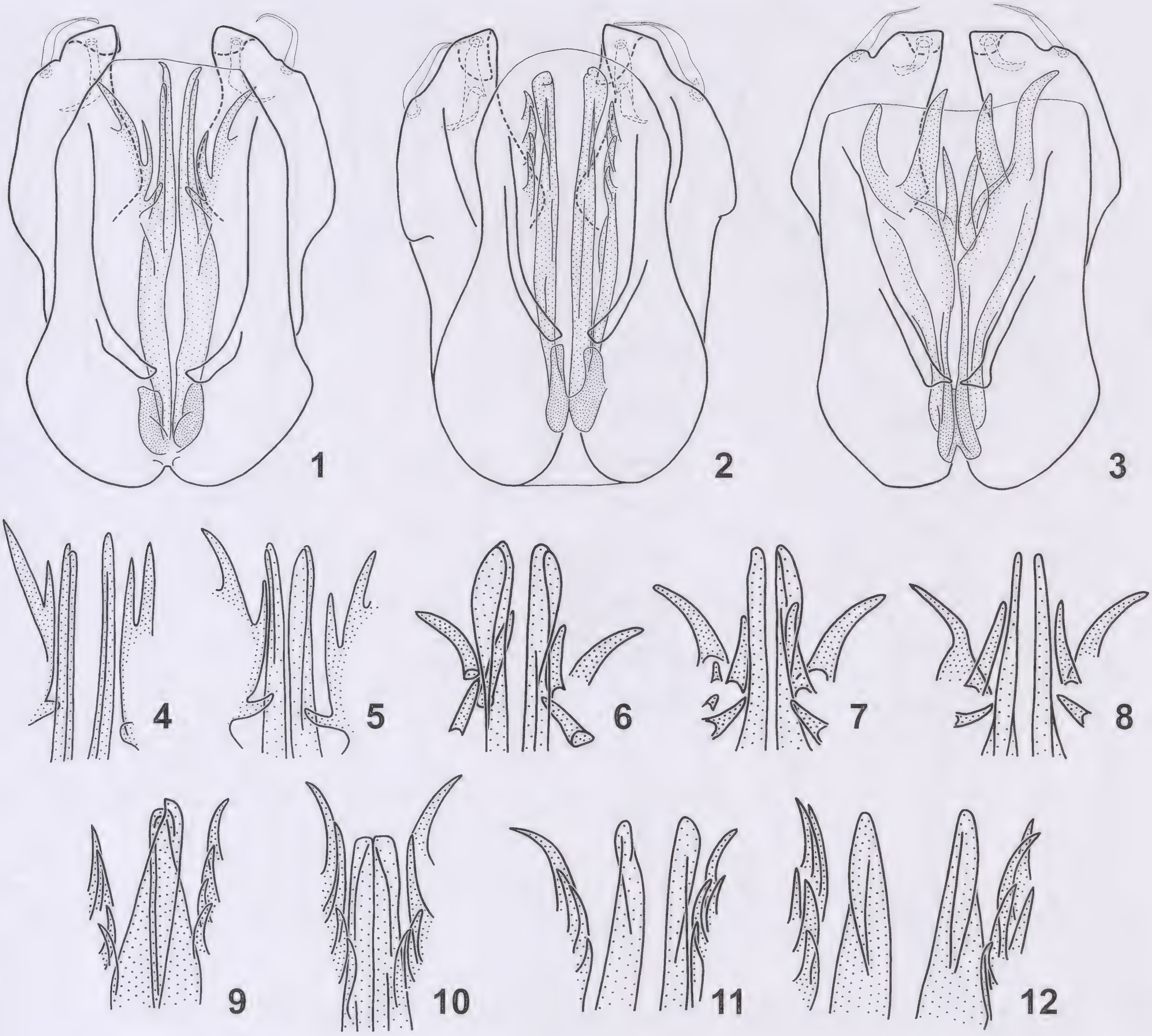
Figs 1, 4-5, 13, 16, 20, 53, 55, 57, 83

Bryaxis excisa L. W. Schaufuss, 1880: 494;
Achilia excisa Jeannel, 1962: 407, 408 fig. 157 (head).
Bryaxis validicornis Reitter, 1885: 325, 328 pl. 2 fig. 9 (head) **syn. nov**.
Achilia validicornis Jeannel, 1962: 407 figs 155 (habitus), 156 (aedeagus). – Jeannel, 1964: 10.

Type material (2 ex.): MNHN (ex coll. Raffray); 1 ♂ (lectotype of *A. excisa,* by present designation); Cuba (labelling mistake). – MNHN; 1 ♂ (lectotype of *A. validicornis*, by present designation); Chili.

Additional material (1432 ex.): See Appendix 1.

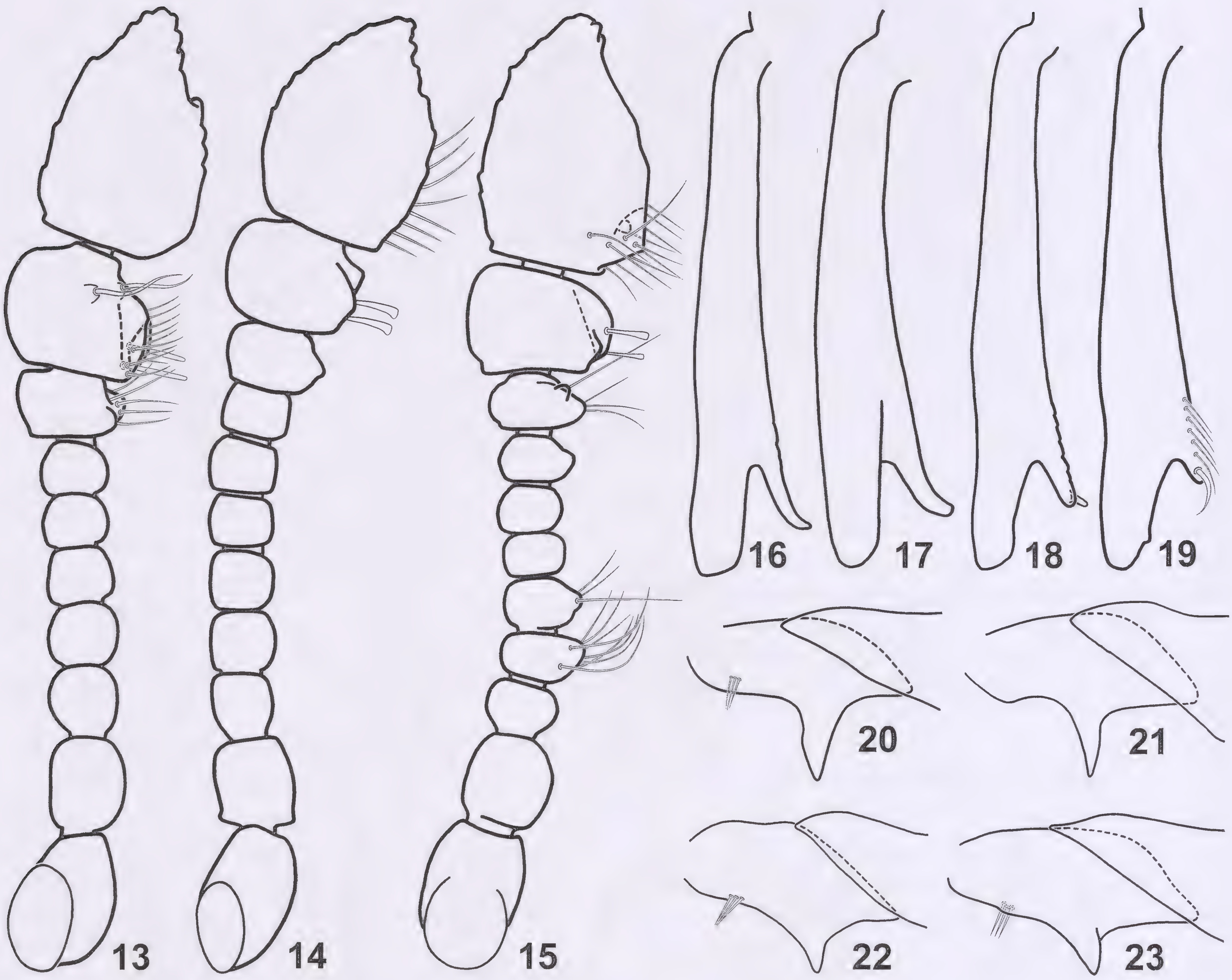
Description: Body 1.35-1.50 mm long, entirely reddish with darker head and palpi yellowish, or with black head, pronotum and abdomen reddish brown, and elytra, antennae, and legs reddish. Head with eyes longer than temples. Pronotum slightly wider than head, with maximal width on anterior half; median antebasal fovea large as lateral ones. First abdominal tergite with basal striae slightly diverging, extending to less than one-third of paratergal length, and separated at base by about one-third of tergal width.
Male: Head as in Figs 53 and 55, flanked on entire length by two deep lateral pits with outer edge toothed at level of eyes (Fig. 57); narrow frontal protuberance slightly convex at base and flattened anteriorly to vertexal sulcus. Antennae (Fig. 13) with scape and pedicel longer than wide; antennomere III as wide as long; antennomeres IV-VIII slightly transverse; antennomeres IX and X strongly transverse with protruding mesal margins bearing long



Figs 1-12. Aedeagi (1-3) and the variability of the internal sac (4-12) of *Achilia*. (1) *A. excisa*, specimen from Contulmo Natural Monument, prov. Malleco. (2) *A. testacea* from Chepu, prov. Chiloé [paratype]. (3) *A. fiura* n. sp., paratype from 17 km W Angol, prov. Malleco. (4) *A. excisa*, specimen from Chepu, prov. Chiloé. (5) *A. excisa*, specimen from Aguas Calientes to Puyehue National Park, prov. Osorno. (6) *A. pachycera*, specimen from Cordillera Nahuelbuta, prov. Malleco [holotype of *Achilia pseudovalidicornis* Franz]. (7) *A. pachycera*, specimen from Nahuelbuta, prov. Malleco. (8) *A. pachycera*, specimen from Nahuelbuta, prov. Malleco. (9) *A. testacea*, specimen from Recinto, prov. Ñuble. (10) *A. testacea*, specimen from Bahia Mansa, prov. Osorno. (11) *A. testacea*, specimen from Recinto, prov. Ñuble. (12) *A. testacea*, specimen from Boca del Bio-Bio, prov. Concepción [holotype of *A. acicularis*].

bristles; antennomere X very large, wider and longer than IX; antennomere XI elongate, as long as VIII-X combined. Metasternum slightly raised in middle, this area with wide median sulcus. Legs with ventral margin of mesotrochanters (Fig. 20) forming long and stout spine; profemora and mesofemora slightly thickened; mesotibiae (Fig. 16) bearing long subbasal spur slightly recurved externally; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrites with faint median impression, all other ventrites flattened at middle; ventrite I with distinct median carina extending from posterior margin to posterior edge of median impression. Aedeagus (Figs 1, 4-5) 0.26-0.30 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically forked and pointed, associated on each side with three pointed sclerites. Parameres very wide with wide and long seta on poorly developed outer lobe; tips strongly recurved posteriorly and bearing wide and long subapical seta.

Female: Similar to male except: head lacking lateral pits; antennomeres IX and especially X shorter and less thickened than for male; antennomere XI as long as



Figs 13-23. Male antennae (13-15), mesotibiae (16-19) and mesotrochanters (20-23) of *Achilia*. (13, 16, 20) *A. excisa*. (14, 19, 22) *A. testacea*. (15, 18, 23) *A. fiura*. (17, 21) *A. pachycera*.

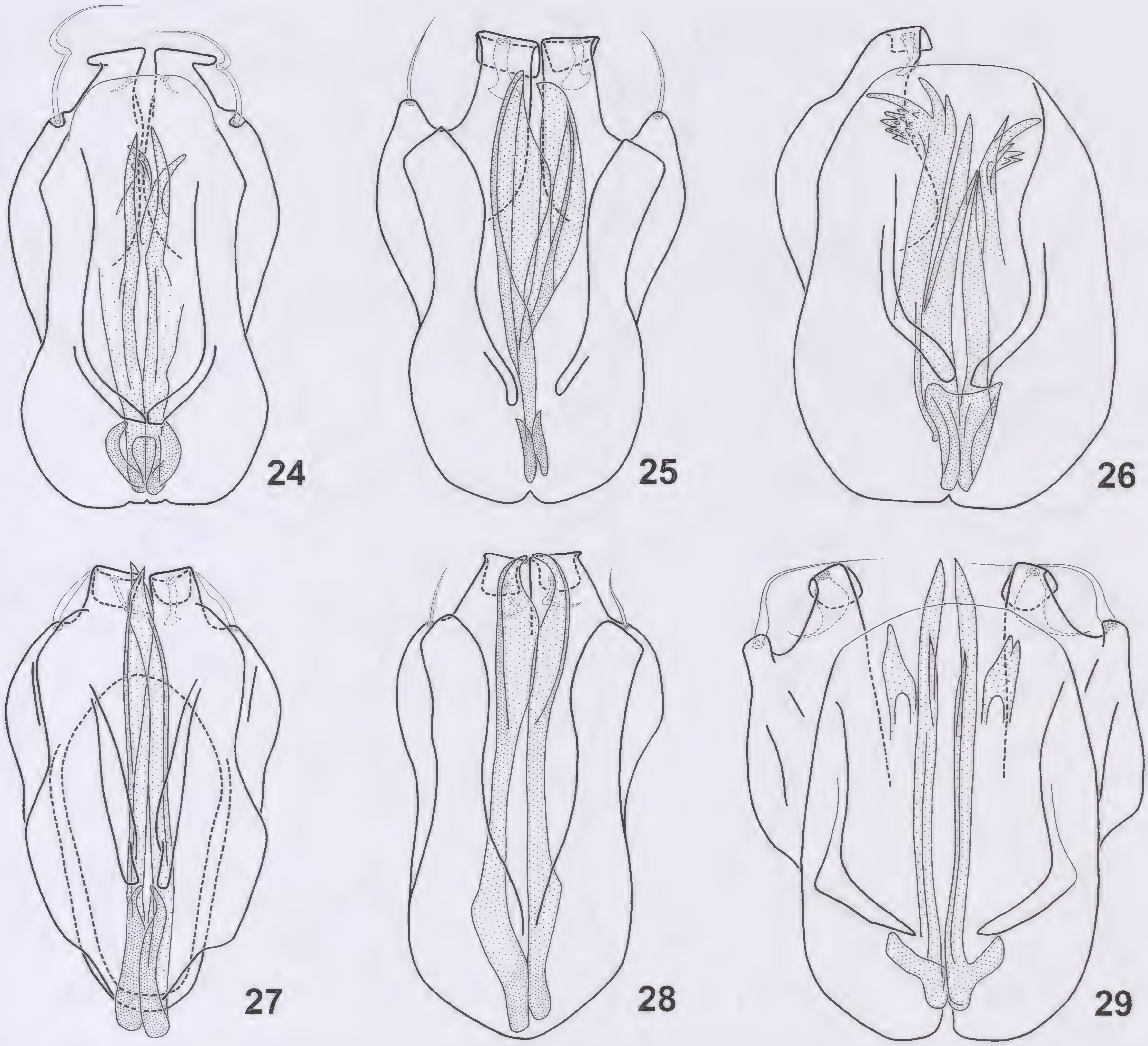
VII-X combined; metasternum, abdominal ventrites, and legs unmodified.

Collecting data: Collected from October to February, mainly in Valdivian rainforests, but also in *Saxegothaea* forests, where it was found also in remnants and in boundary forests at elevations ranging from sea level to 1000 m. Most specimens came from sifted samples of leaf and log litter, moss, dead trunks, vegetable debris and sometimes mushrooms, and from flight intercept traps. Rarely collected by windows traps and car nets.

Distribution: *Achilia excisa* is relatively common (Fig. 83: red circles) in the central region of Chile from Chiloé Province to Malleco Province. In the MNHN we have examined 3 females from Zaparral 20.IX.1957, G. Kuschel (Región Valparaíso, Petorca Province) belonging to the *A. frontalis* group, which, lacking the males, we cannot attribute with certainty to any species.

Comments: Schaufuss (1880: 494) described *Bryaxis excisa* based on three specimens, two labelled as being from Cuba, whose provenance was guaranteed by Zahlmeister Riehl, and one from Chile, with whose provenance Schaufuss had doubts. Reitter (1885: 325, 328) described *Bryaxis validicornis* on the basis of two males collected in Valdivia, one by Lady Kindermann and the other by Riehl, but he did not mention *Bryaxis excisa.* Jeannel (1962: 407-408) redescribed these two species under the generic name *Achillia* (misspelling), and distinguished them from others by the form of the lateral pits of the head: reaching beyond the posterior edge of the eyes and with the lateral margin not toothed in *A. excisa*, and not reaching the posterior edge of the eyes and with the lateral margin toothed in *A. validicornis*.

Concerning *Achilia excisa* Jeannel (1962: 408) considered it unlikely that it was from Cuba, and asserted that it was certainly collected in Chile, despite mentioning the type, preserved in MNHN, was labelled as being from Cuba.

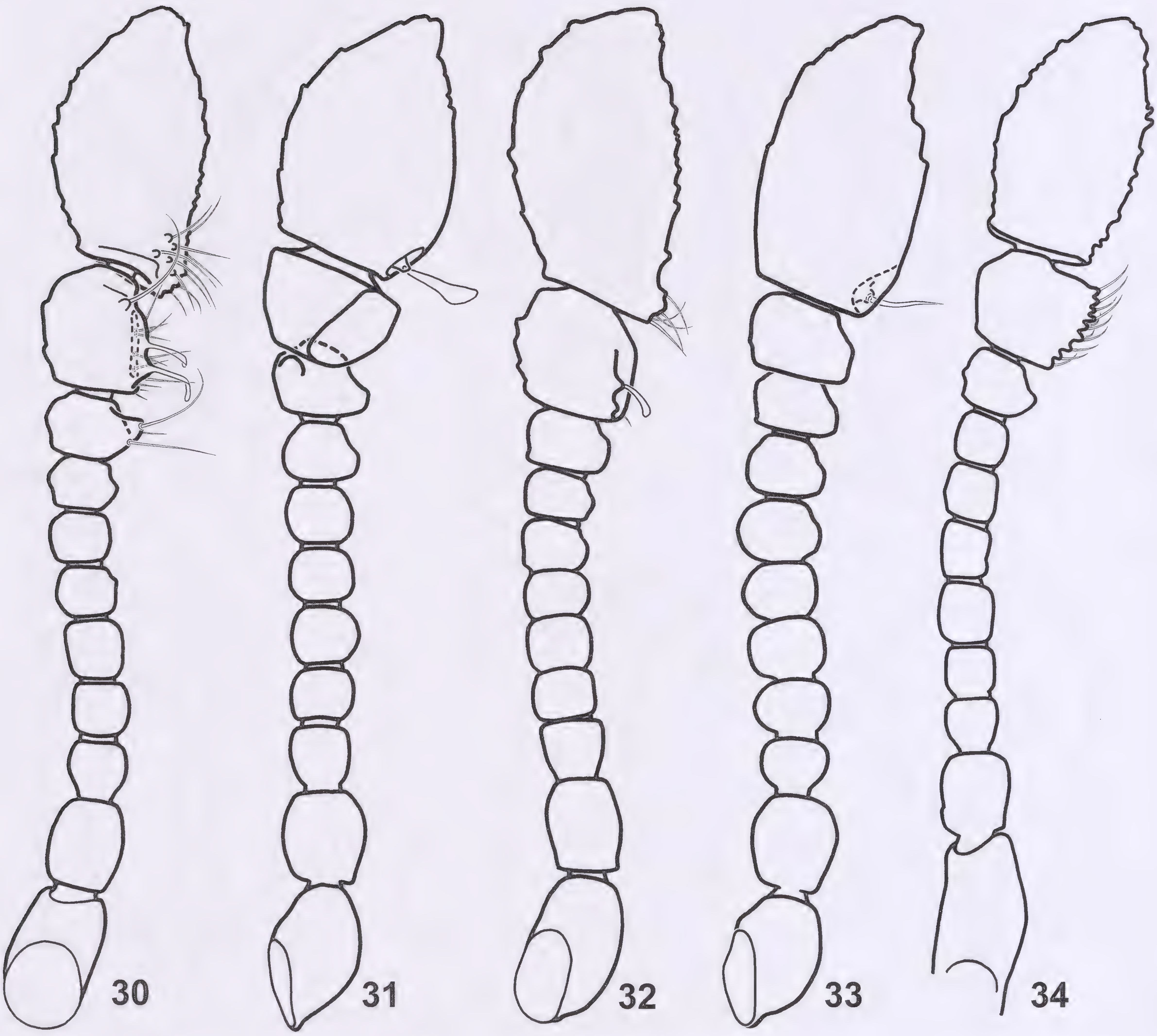


Figs 24-29. Aedeagi of *Achilia*. (24) *A. caracolana*, specimen from Hualpèn, prov. Concepción. (25) *A. auriculata*, specimen from Peniquillo, prov. Concepción. (26) *A. ovallensis*, specimen from Ovalle, prov. Limarí [paratype]. (27) *A. frontalis*, specimen from Aguas Calientes to Puyehue National Park, prov. Osorno. (28) *A. trauco*, specimen from 34 km WNW La Union, prov. Ranco [paratype]. (29) *A. longispina*, specimen from Mina de la Disputada, prov. Valparaíso.

We examined all the material of the MNHN collection and found in Raffray's collection one specimen of *A. excisa* labelled as "Cuba/Type [red label]/*A. excisa* Raffray det.", and one specimen of *A. validicornis* labelled as "Chili/Type [red label]/ *A. validicornis* Raffray det.". We consider these two male as the lectotypes of *A. excisa* and *A. validicornis*, respectively, and have labelled them accordingly.

The aedeagi of the two above-mentioned specimens are partially damaged, nevertheless they appear similar in respect to both the shape of the parameres and the structure of copulatory pieces. Our study of the very abundant additional material shows also that the differences highlighted by Jeannel in the features of the head between *A. excisa* and *A. validicornis* were overestimated and pertain to intraspecific variation, and particularly that the lateral pits of the male of the lectotype of *A. excisa* are toothed at level of eyes; consequently we here place *A. validicornis* (Reitter, 1885) as the junior synonym of *A. excisa* (Schaufuss, 1880) (**syn. nov.**).

Achilia excisa is a very common species in Central Chile, and the genus is so far unknown outside of central and southern Chile and southern Argentina. Thus we consider that the occurrence of this species in Cuba can be ruled out with a high level of confidence, and that this locality record is most likely due to a labelling mistake.



Figs 30-34. Male antennae of *Achilia*. (30) *A. caracolana*. (31) *A. auriculata*. (32) *A. ovallensis*. (33) *A. frontalis*. (34) *A. longispina*.

Achilia pachycera Jeannel, 1963
Figs 6-8, 17, 21, 83

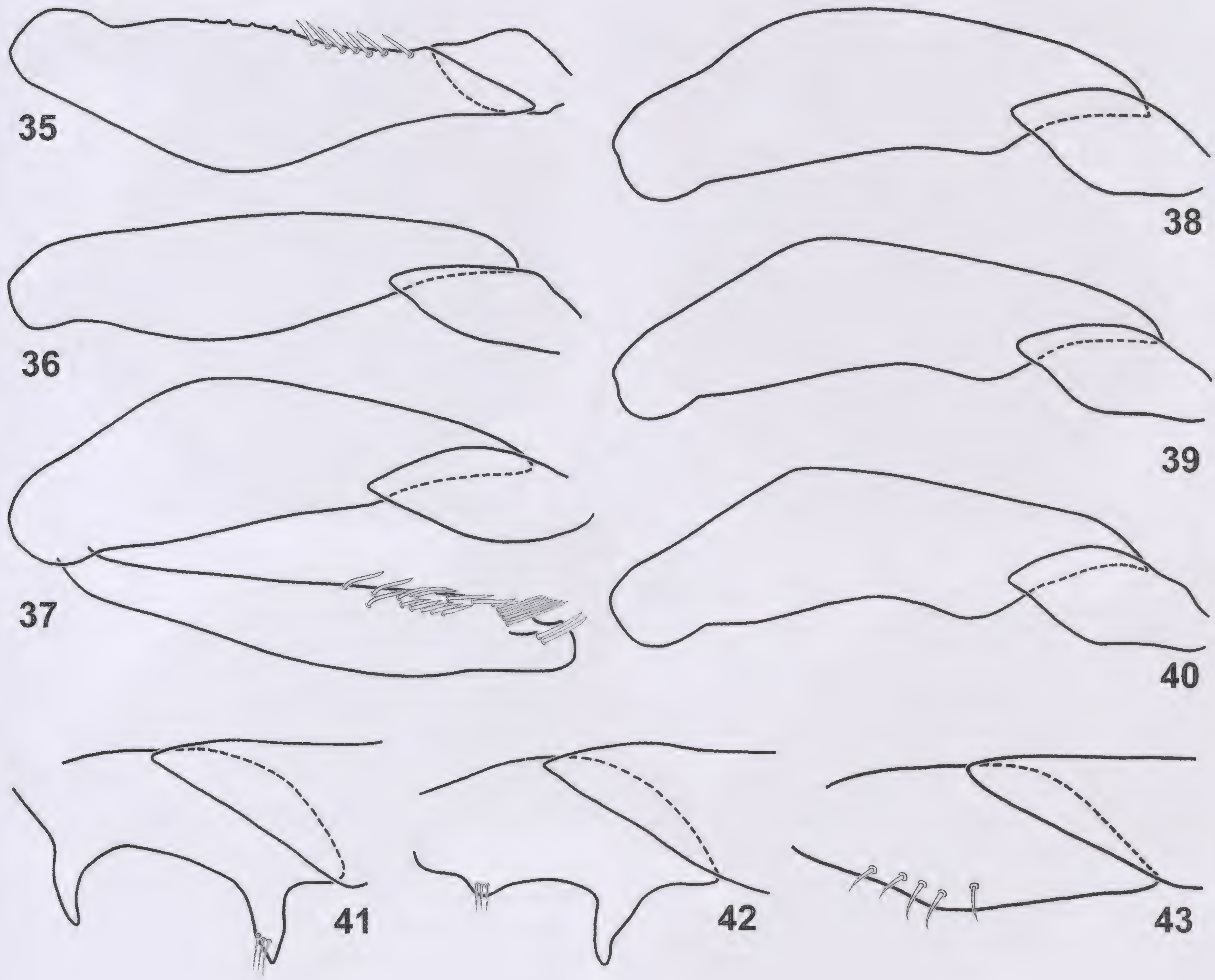
Achilia pachycera Jeannel, 1963: 353, 363 figs 10 (head and antennae), 11 (aedeagus). – Jeannel, 1964: 10.
Achilia pseudovalidicornis Franz, 1996: 116 fig. 64 (aedeagus) **syn. nov**.

Type material (5 ex.): CENTRAL CHILE: Región Araucanía: Malleco prov.: MNHN; 1 ♂ (holotype of *A. pachycera*); Nahuelbuta; 1961; F. Castri. – MNHN; 1 ♂ and 2 ♀ (paratypes of *A. pachycera*); same data; F. Castri. – NHMW (coll. Franz); 1 ♂ (holotype of *A. pseudovalidicornis*); National Park of Nahuelbuta; Cordillera Nahuelbuta; 04.XI.1986; H. Franz.

Additional material (150 ex.): See Appendix 1.

Description: Body 1.40-1.50 mm long, usually entirely reddish with black head and palpi yellowish, sometimes with abdomen and pronotum reddish brown. Head with eyes longer than temples. Pronotum wider than head, with maximal width on anterior half; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae slightly diverging, extending to about one-third of paratergal length, and separated at base by more than one-third of tergal width.

Male: Head similar to *A. excisa*, flanked on entire length by two very deep pits with outer edge toothed at level of eyes; narrow frontal protuberance slightly convex at base, and distinctly flattened and enlarged anteriorly up to vertexal sulcus. Antennae similar to *A. excisa* (see Fig. 13). Metasternum with large median impression; posterior margin densely pubescent. Legs with ventral margin of mesotrochanters (Fig. 21) forming long and thin spine; profemora and mesofemora slightly thickened; mesotibiae (Fig. 17) bearing subbasal spur slightly recurved externally and apically rounded; metatibiae slightly sinuate on distal half. Abdominal



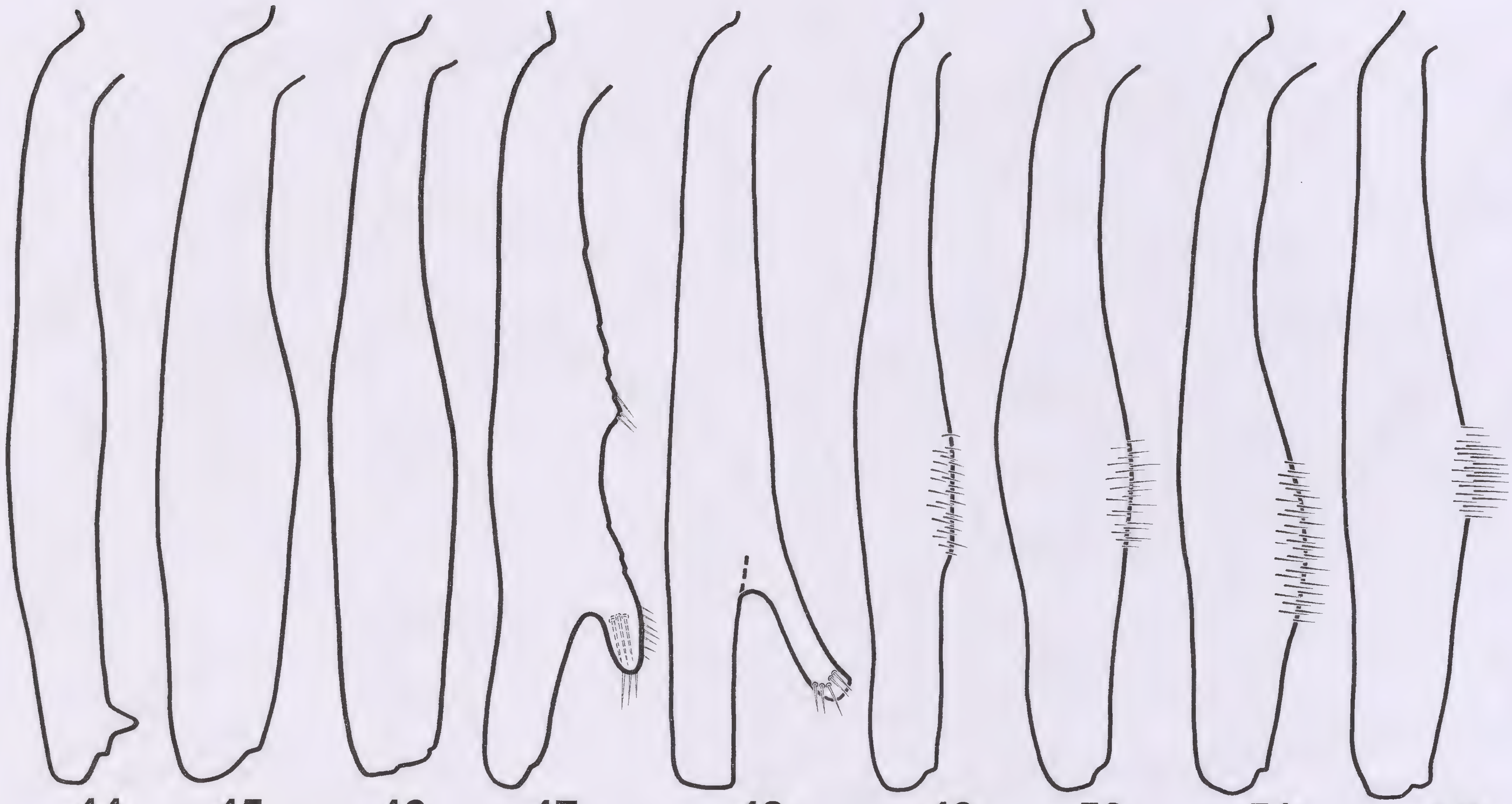
Figs 35-43. Male profemur (35), metafemur (36), the variability of metafemur (38-40), metaleg (37) and mesotrochanter (41-43) of *Achilia*. (35, 41) *A. caracolana*. (36) *A. trauco*. (37) *A. frontalis*, specimen from Chillàn. (38) *A. frontalis*, specimen from Cordillera de Nahuelbuta. (39) *A. frontalis*, specimen from Frutillar. (40) *A. frontalis*, specimen from Aguas Calientes to Puyehue National Park. (42) *A. ovallensis* [paratype]. (43) *A. longispina*.

tergites unmodified; first abdominal ventrites with deep median impression with raised edges; all other ventrites distinctly flattened at middle; ventrite I with short median carina extending from posterior margin to posterior edge of median impression. Aedeagus 0.26-0.30 mm long; similar to *A. excisa* (see Fig. 1), except copulatory pieces (Figs 6-8) consisting of pair of long medial sclerites recurved and strongly sclerotised at base, apically enlarged or pointed, and associated on each side with three or sometimes more short pointed sclerites. Parameres very wide with long seta on poorly developed outer lobe; tips strongly recurved posteriorly and bearing wide and long subapical seta.
Female: Similar to male except: head lacking lateral pits; antennomeres IX and especially X shorter and less enlarged than male; metasternum, abdominal ventrites, and legs unmodified.

Collecting data: Collected from November to February in *Nothofagus* and *Araucaria* forests, where it was found from 1100 m to 1300 m. Most specimens came from sifted samples of leaf and log litter, moss, dead trunks, vegetable debris; two specimens were collected by flight intercept traps.

Distribution: *Achilia pachycera* is known only from the Nahuelbuta District (Malleco Province, Araucanía Region) (Fig. 83: blue triangles).

Comments: Jeannel (1963: 353) first mentioned *A. pachycera* as a member of the *A. spinifer* group, however some pages later (1963: 363-364) he correctly places it as a member of his *A. frontalis* group.
According to Jeannel (1964: 10), *A. pachycera* is very similar to *A. validicornis* (now a junior synonym of *A. excisa*), from which it differs by the shape of the male



Figs 44-52. Male protibia (44-46) and mesotibia (47-52) of *Achilia*. (44, 47) *A. caracolana*. (45, 50) *A. frontalis*. (46, 51) *A. trauco*. (48) *A. ovallensis*. (49) *A. auriculata*. (52) *A. longispina*.

frontal protuberance (anteriorly widened in *A. pachycera*, and constricted in *A. validicornis*).

From the abundant material we studied, we could not separate the females of the two species, while the males can be distinguished by the following characters: frontal protuberance of head anteriorly more enlarged in *A. pachycera*, lateral pits of head of *A. pachycera* generally deeper and with larger tooth on their outer margin than in *A. excisa*, features of mesotrochanters (cf. Figs 20, 21) and mesotibiae (cf. Figs 16, 17) slightly different, as well as metasternum (with medial sulcus in *A. excisa*, and bearing a large impression in *A. pachycera*) and abdominal ventrites (slightly flattened at middle for *A. excisa*, clearly flattened for *A. pachycera*). *Achilia pachycera* also differs from *A. excisa* by the morphology of the copulatory pieces of the aedeagus, which exhibit constant and stable differences, especially with respect to the location of the three pointed pairs of internal sclerites, which are either fused (Figs 1, 4-5) or disconnected (Figs 6, 8). Within the light of these slight but nevertheless constant differences, we consider it appropriate to maintain *A. pachycera* as a valid species.

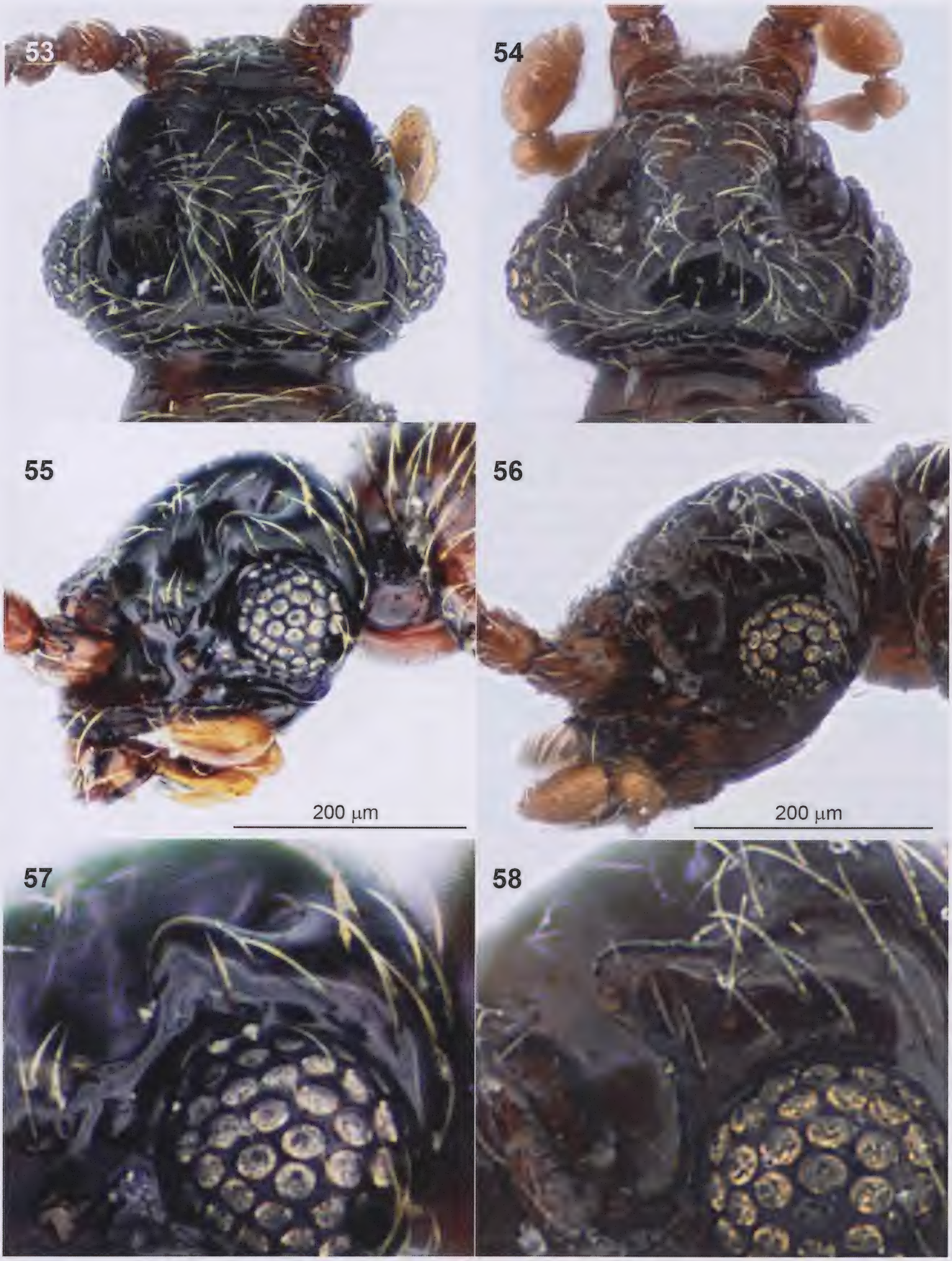
Examination of the holotype and only known specimen of *A. pseudovalidicornis* revealed that both external and aedeagal characters fit perfectly our concept of *A. pachycera* Jeannel, 1963. Therefore we conclude that *A. pseudovalidicornis* Franz, 1996 must be considered to be a junior synonym of *A. pachycera* Jeannel, 1963 (**syn. nov.**).

Achilia fiura n. sp.

Figs 3, 15, 18, 23, 54, 56, 58, 83

Type material (13 ex.): CENTRAL CHILE: Región Araucanía: Malleco prov.: MHNG; 1 ♂ (holotype); 45 km W Angol; 1400 m; 09.XII.1984/16.II.1985; S. & J. Peck; *Nothofagus* forest litter, car trap. – MHNG; 5 ♂ (paratypes); same data; S. & J. Peck; *Nothofagus* forest litter, car trap. – MNHS; 1 ♂ (paratype); same data; S & J. Peck; Nothofagus forest litter; car trap. – MHNG; 2 ♂ (paratypes); Nahuelbuta National Park, 40 km W Angol; 1200-1500 m; 19.XII.1984/17.II.1985; S. & J. Peck; *Nothofagus-Araucaria*; for FIT. – MHNG; 3 ♂ (paratypes); 17 km W Angol; 800 m; 08.XII.1984/16. II.1985; S. & J. Peck; FIT mixed *Nothofagus*. – FMNH (FMHD #2002-95); 1 ♂ (paratype); Nahuelbuta National Park, 2.3 km W Los Portones entrance; 37° 49.41'S 72° 58.95'W; 1150 m; 25.XII.2002; Solodovnikov 1057; *Nothofagus dombeyi + antarctica*, mostly open understory, berlese, leaf & log litter, forest floor.

Description: Body 1.45-1.50 mm long, usually entirely reddish with darker head and abdomen, and palpi yellowish. Head with eyes longer than temples. Pronotum wider than head, with maximal width on anterior half; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae slightly diverging, extending to less than one-third of paratergal length, and separated at base by more than one-third of tergal width.



Figs 53-58. (53, 55, 57) *Achilia excisa*. (54, 56, 58) *A. fiura*. Male head in (53-54) dorsal and (55-56) lateral views. (57-58) male supraocular area in lateral view. Scale bar left for (53, 55) and right for (54, 56).

Male: Head as in Figs 54 and 56, flanked on entire length by two very deep pits with outer edge toothed at level of eyes (Fig. 58). Narrow frontal protuberance slightly convex at base and anteriorly flattened to vertexal sulcus. Antennae (Fig. 15) with scape and pedicel longer than wide; antennomere III wider than long; antennomere IV transverse, with protruding mesal margin pointed in middle and bearing a tuft of long setae; antennomere V transverse, with protruding mesal margin pointed in middle and bearing a long seta; antennomeres VI-VII distinctly wider than long; antennomere VIII transverse, with protruding mesal margin; antennomeres IX and X strongly transverse, with protruding mesal margin bearing long setae; antennomere X wider and longer than IX; antennomere XI elongate and longer than VIII-X combined, its medial margin enlarged at base and bearing a tuft of long setae. Metasternum with large median impression. Legs with ventral margin of mesotrochanters (Fig. 23) forming short median spine; profemora and mesofemora slightly thickened; mesotibiae (Fig. 18) forming subbasal spur slightly recurved externally and with short stout apical seta; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrites with faint median impression, all other ventrites flattened at middle; ventrite I with short median carina extending from posterior margin the posterior edge of median impression. Aedeagus (Fig. 3) 0.28-0.30 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically pointed, associated on each side with sclerite ending with two large spines. Parameres very wide with long seta on well-developed outer lobe; tips strongly recurved posteriorly and bearing wide subapical seta.
Female: Unknown.

Collecting data: Collected from December to February in *Nothofagus* and *Araucaria* forests, where it was found from 1150 m to 1500 m. Most specimens were taken by flight intercept traps and by car netting; one specimen was collected in sifted samples of leaf and log litter.

Distribution: *Achilia fiura* is known only from Malleco Province (Región Araucanía) (Fig. 83: green diamonds).

Comments: *Achilia fiura* is very similar to *A. excisa* and *A. pachycera*, from which it is easily distinguished by the male features of the antennae (compare Figs 13 and 15), mesotrochanters (compare Figs 20, 21 and 23), mesotibiae (compare Figs 16, 17 and 18), and the copulatory pieces of the aedeagus (compare Figs 1 and 4-5; 6-8, and 3).

Achilia testacea Jeannel, 1962

Figs 2, 9-12, 14, 19, 22, 59-64, 84

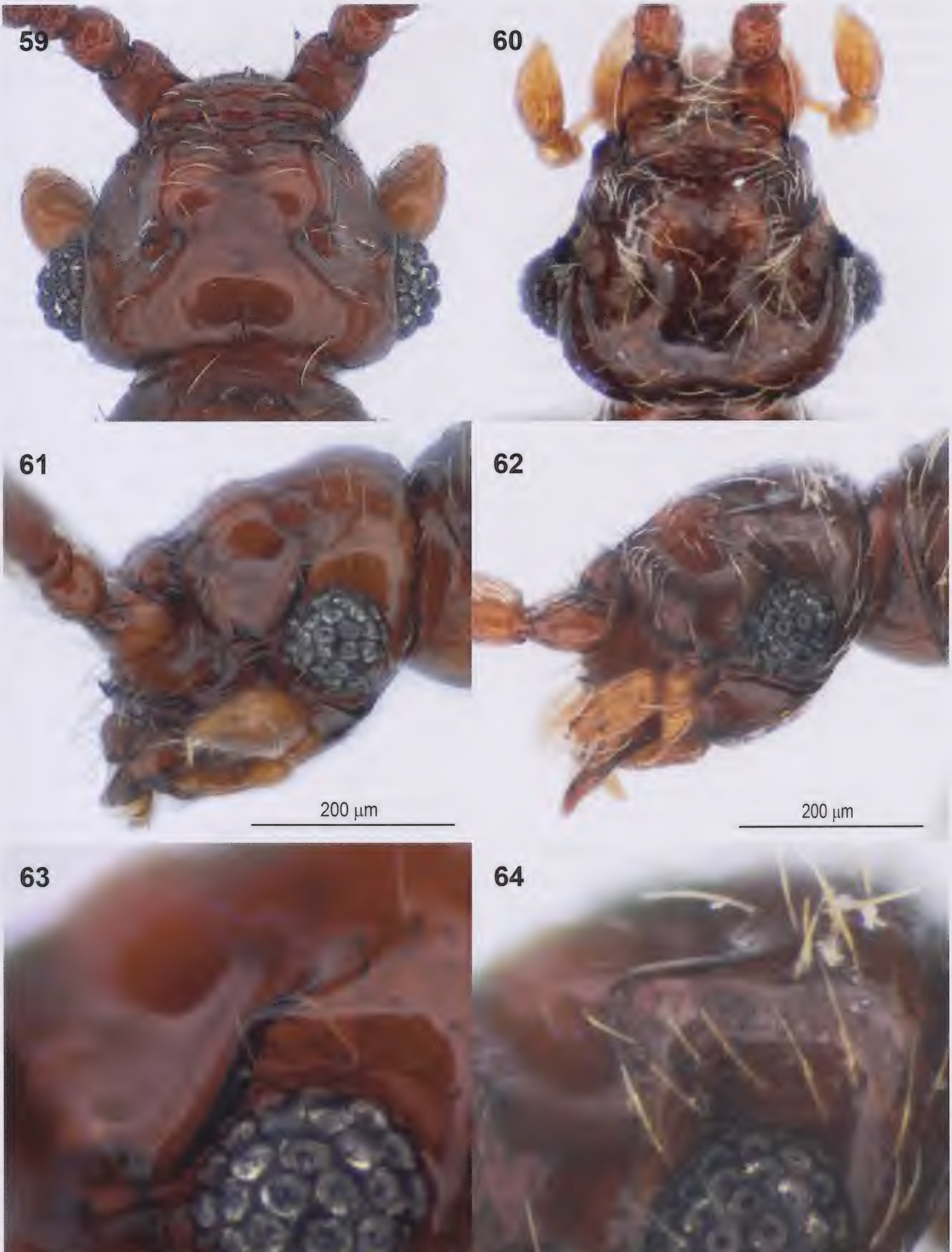
Achillia testacea Jeannel, 1962: 409, 411 figs 158 (habitus), 159 (aedeagus).

Achillia acicularis Jeannel 1962: 409, 412 fig. 160 (aedeagus) **(syn. nov.)**

Type material (4 ex.): CENTRAL CHILE: Región Los Lagos: Chiloé prov.: MHNS; 1 ♂ (holotypes of *Achilia testacea* n° 1690); Chiloé Island, Chepu; 02.X.1958; G. Kuschel. – MNHN; 1 ♂ and 1 ♀ (paratypes of *Achilia testacea*); Chiloé Island, Chepu; 42° 03'S; 15.X.1958; G. Kuschel. – Región Bío Bío: Concepción prov.: MNHN; 1 ♂ (holotype of *Achilia acicularis*); Bocas of Bío Bío; 36° 50'S; 24.V.1957; G. Kuschel.

Additional material (103 ex.): See Appendix 1.

Description: Body 1.45-1.55 mm long, entirely reddish with palpi yellowish. Head with eyes longer than temples. Pronotum wider than head, with maximal width on anterior half; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae diverging, extending to about half of paratergal length, and separated at base by more than one-third of tergal width.
Male: Head as in Figs 59-62, at eye level with simple flattening of the lateral region surmounted by small tooth (Fig. 63), or flanked by lateral pits with outer margin toothed at eye level (Fig. 64). Large frontal protuberance slightly convex at base and anteriorly barely flattened to vertexal sulcus. Antennae (Fig. 14) with scape and pedicel longer than wide; antennomere III slightly longer than wide; antennomeres IV and V as long than wide; antennomeres VI-VIII distinctly wider than long; antennomere IX transverse, with protruding mesal margin pointed at middle; antennomere X wider and longer than IX, with protruding mesal margin bearing two long and large setae; antennomere XI elongate and longer than VIII-X combined, its mesal margin bearing long setae. Metasternum with large median impression. Legs with ventral margin of mesotrochanters (Fig. 22) forming short spine; profemora and mesofemora slightly thickened; mesotibiae (Fig. 19) bearing short and densely pubescent subbasal spur; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrite raised at middle, other ventrites weakly flattened at middle; surface of ventrite I with marked long median carina extending from posterior margin to about its midlength. Aedeagus (Fig. 2) 0.25-0.28 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically rounded, associated on each side with four or five pointed sclerite. Parameres very wide with wide and long seta on poorly developed outer lobe; tips broadly recurved posteriorly and bearing wide and long subapical seta.
Female: Similar to male except: head not modified; antennomeres IX and especially X shorter and less protruding than for male; metasternum, abdominal ventrites, and legs unmodified, except ventral margin of mesotrochanters bearing very short spine.



Figs 59-64. *Achilia testacea*. Male head in (59-60) dorsal and (61-62) lateral views. (63-64) male supraocular area in lateral view. Scale bars left for (59, 61) and right for (60, 62).

Collecting data: Collected from September to May in Valdivian rainforests, also in remnants and disturbed forests, where it was found from sea level to 450 m. All specimens were collected from sifted samples of leaf and log litter and/or debris.

Distribution: *Achilia testacea* is known from Central Chile, ranging from Chiloé Province to Ñuble Province (Fig. 84: orange discs).

Comments: The males of *A. testacea* exhibit great variability in the morphology of the head: some males, including the holotype and the paratype, have at the eye level a simple flattening of the lateral region surmounted by a small tooth, while others have true lateral pits with the outer margin toothed. All of these males share the morphology of the antennae, metasternum, abdominal ventrites, and legs; and their aedeagi have identical dorsal plates and parameres, with the copulatory pieces characterised by little variation (cf. Figs 2, 9-11).
According to Jeannel (1962: 409), *A. acicularis* differs from *A. testacea* only by the features of the head of male (with lateral pits in *A. acicularis,* without lateral pits in *A. testacea*). Comparison of the holotype of *A. acicularis* and a paratype of *A. testacea* showed that their aedeagal conformation is very similar (cf. Figs 2 and 12). It is the same for the morphology of their antennae and legs, and the difference in the morphology of their head, according to us, may be attributed to intraspecific variation of this taxon. Therefore we conclude that *A. acicularis* Jeannel, 1962 must be placed as a junior synonym of *A. testacea* Jeannel, 1962 (**syn. nov.**).

Achilia caracolana Jeannel, 1962

Figs 24, 30, 35, 41, 44, 47, 65, 67, 69, 84

Achilia caracolana Jeannel, 1962: 409 fig. 163 (aedeagus).

Type material (7 ex.): CENTRAL CHILE: Región Bío Bío: Concepción prov.: MHNS; 1 ♂ (holotype of *Achilia caracolana* n° 1685); Cerro Caracol; 24.V.1957; G. Kuschel. – MNHN; 2 ♂ and 4 ♀ (paratypes); Cerro Caracol; 36° 50'S; 23.V.1957; G. Kuschel.

Additional material (318 ex.): See Appendix 1.

Description: Body 1.5-1.8 mm long, entirely reddish or reddish brown, with palpi yellowish. Head with eyes longer than temples. Pronotum slightly wider than head, with maximal width on anterior half; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae parallel, extending to about quarter of paratergal length, and separated at base by more than one-third of tergal width.
Male: Head as in Figs 65 and 67, with deep lateral pits surmounted on each side of eyes by small tooth apically truncated (Fig. 69); large frontal protuberance convex with distinct V-shaped median impression reaching anteriorly to vertexal sulcus. Antennae (Fig. 30) with scape and pedicel longer than wide; antennomere III as long as wide; antennomere IV slightly wider than long; antennomere V slightly longer than wide; antennomeres VI-VIII distinctly wider than long; antennomere IX transverse with protruding mesal margin pointed at middle and bearing two long setae; antennomere X barely longer than wide, wider and longer than IX, with mesal margin apically hollowed, basally projecting and bearing two long and large setae as well as a tuft of shorter setae; antennomere XI elongate, longer than VIII-X combined, its medial margin bearing long subbasal setae. Metasternum with deep and broad ovoidal median impression, posterior edges of the latter densely pubescent. Legs with ventral margin of mesotrochanters (Fig. 41) bearing two short spines; profemora (Fig. 35) strongly thickened, with ventral margin finely denticulate and bearing short modified setae on basal third; mesofemora slightly thickened; protibiae (Fig. 44) slightly thickened with mesal margin bearing small subapical spine; mesotibiae (Fig. 47) thickened with mesal margin bulging at middle and bearing apically pubescent subbasal spur; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrites with large median impression, all other ventrites flattened at middle; ventrite I with short median carina extending from posterior margin to posterior edge of median impression. Aedeagus (Fig. 24) 0.30-0.325 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically bifid. Parameres wide with very long seta on poorly developed outer lobe; tips strongly recurved posteriorly and bearing thin and short subapical seta.
Female: Similar to male except: head, metasternum, abdominal ventrites, and legs unmodified; antennomeres IX and specially X shorter and less thickened than male.

Collecting data: Collected from September to May in *Nothofagus*, *Cupressus* and *Eucalyptus* forests; also in remnants, where it was found from sea level to about 1200 m. Most specimens were collected from sifted samples of leaf and log litter.

Distribution: *Achilia caracolana* is known from Central Chile, ranging from Chiloé Province to Talca Province (Fig. 84: green diamonds).

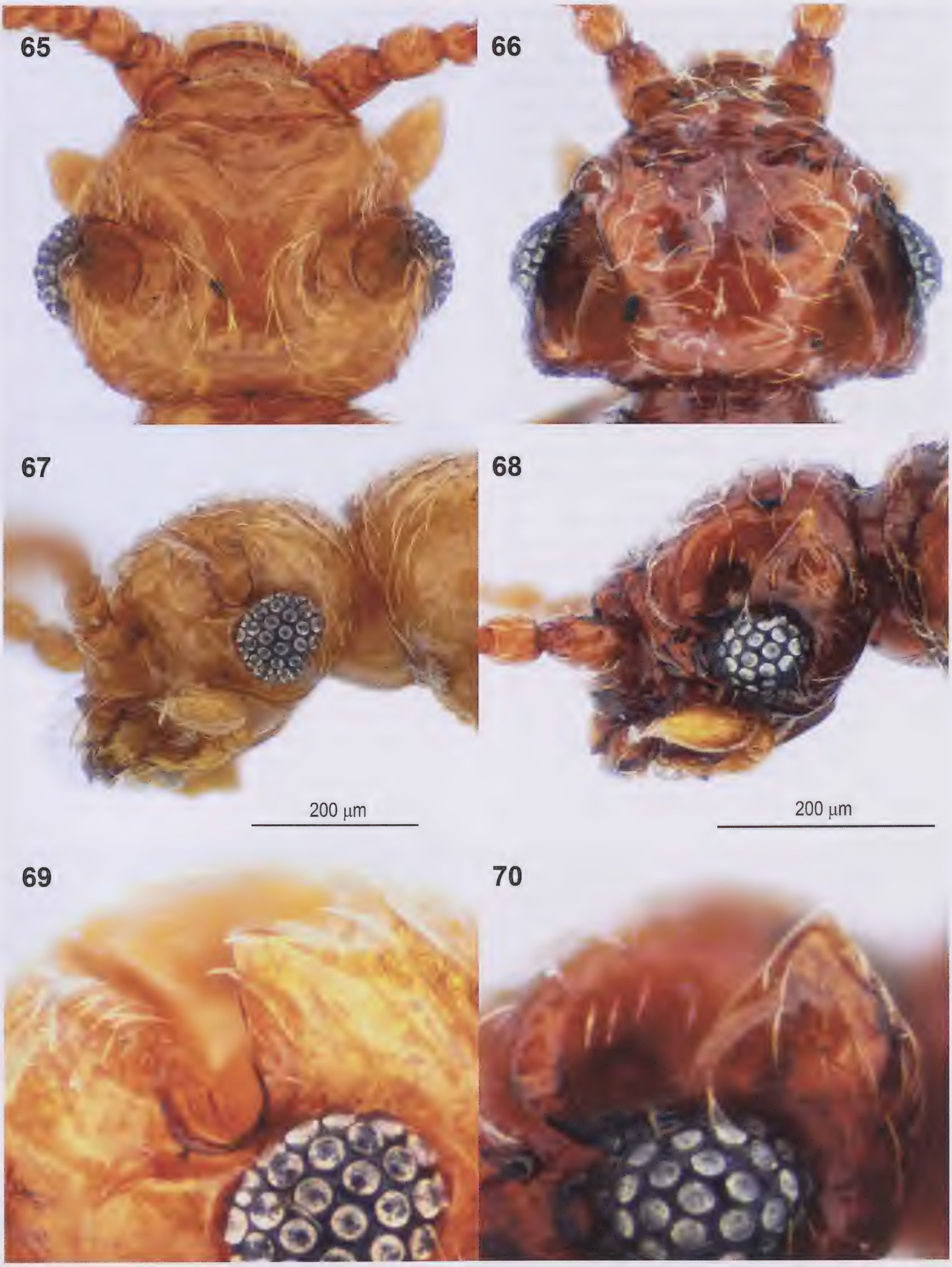
Achilia auriculata Jeannel, 1962

Figs 25, 31, 49, 66, 68, 70, 83

Achilia auriculata Jeannel, 1962: 409, 410 fig. 164 (aedeagus).

Type material (2 ex.): CENTRAL CHILE: Región Bío Bío: Ñuble prov.: MNHN; 2 ♂ (holotype and paratype); Chillàn; 36° 54'S; P. Germain.

Additional material (4 ex.): See Appendix 1.



Figs 65-70. (65, 67, 69) *Achilia caracolana*. (66, 68, 70) *A. auriculata*. Male head in (65-66) dorsal and (67-68) lateral views. (69-70) male supraocular area in lateral view. Scale bar left for (65, 67) and right for (66, 68).

Description: Body 1.25-1.35 mm long, entirely reddish brown with darker abdomen and palpi yellowish. Head with eyes as long as temples. Pronotum narrower than head, with maximal width at midlength; median antebasal fovea smaller than lateral ones. First abdominal tergite with basal striae parallel, extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.
Male: Head as in Figs 66 and 68, wider than pronotum, on each side with large lateral pit open behind and outer margin forming big tooth above eyes (Fig. 70); large frontal protuberance barely convex. Antennae (Fig. 31) with scape and pedicel longer than wide; antennomere III as long as wide; antennomeres IV-VIII wider than long; antennomere VIII with mesal margin protruding; antennomere IX transverse with mesal margin protruding; antennomere X strongly transverse, wider and longer than IX, wider than XI, with mesal side truncate and bearing broad flat area; antennomere XI elongate and longer than VIII-X combined, bearing long and large subbasal seta inserted in deep depression. Metasternum with median impression. Legs with profemora and mesofemora slightly thickened; mesotibiae (Fig. 49) with very small subapical tooth, in middle slightly bulging and bearing tuft of short setae; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrite raised at middle, remaining ventrites slightly flattened at middle; ventrite I with short median carina extending from posterior margin to about quarter of its length. Aedeagus (Fig. 25) 0.24-0.25 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically slightly narrowed and pointed. Parameres wide with very long seta on poorly developed outer lobe; tips strongly recurved posteriorly and bearing short and thin subapical seta.
Female: Similar to male except: head unmodified, narrower than pronotum; antennomeres IX and especially X shorter and less thickened than male; metasternum, abdominal ventrites, and legs unmodified.

Collecting data: This species was collected from September to January at moderate elevations. The only ecological data available refers to a sample processed by a Berlese funnel, that consisted of leaf & log litter taken from the forest floor of a subtropical xerophytic forest.

Distribution: *Achilia auriculata* is known only from Bío Bío Region (Ñuble and Concepción Provinces) in Central Chili (Fig. 83: pink squares).

Achilia ovallensis Jeannel 1962

Figs 26, 32, 42, 48, 83

Achilia ovallensis Jeannel, 1962: 409, 413 fig. 162 (aedeagus).

Type material (4 ex.): CENTRAL-NORTHERN CHILE: Región Coquimbo: Limarí prov.: MHNS; 1 ♀ (holotype of *Achilia ovallensis* n° 1695); Ovalle; P. Germain. – MNHN; 1 ♂ and 2 ♀ (paratypes); Ovalle; 30° 36'S; P. Germain.

Additional material (3 ex.): See Appendix 1.

Description: Body 1.5-1.55 mm long, entirely reddish with palpi yellowish. Head with eyes shorter than temples. Pronotum slightly wider than head, with maximal width at midlength; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae slightly divergent, extending to about one-quarter of paratergal length, and separated at base by about one-third of tergal width.
Male: Head similar to *A. testacea*, with simple flattening of lateral regions surmounted by small tooth at level of eyes; frontal protuberance basally convex and anteriorly flattened to vertexal sulcus. Antennae (Fig. 32) with scape and pedicel longer than wide; antennomere III as long as wide; antennomeres IV-VIII wider than long; mesal margin of antennomeres VII and VIII protruding; antennomere IX transverse with mesal margin protruding; antennomere X as long as wide, wider and longer than IX, with ridge bearing large and short seta; antennomere XI elongate, longer than VII-X combined, mesally bearing few long subbasal setae. Metasternum with deep ovoidal median impression, posterior edge of the impression pubescent. Legs with ventral margin of mesotrochanters (Fig. 42) forming stout spine; profemora and mesofemora slightly thickened; medial edge of mesotibiae (Fig. 47) on basal third forming conspicuous blunt projection bearing subapical tufts of short setae, at middle slightly bulging and bearing tuft of short setae; metatibiae slightly sinuate on distal half. Abdominal tergites unmodified; first abdominal ventrite impressed at middle, remaining ventrites flattened at middle; ventrite I with median carina extending from posterior margin to posterior edge of median impression. Aedeagus (Fig. 26) 0.325 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites recurved and strongly sclerotised at base, and apically bifid with each side associated with sclerite forming three large tips and numerous additional spinules. Parameres wide with long seta on poorly developed outer lobe; tips strongly recurved posteriorly and bearing wide subapical seta.
Female: Similar to male except: head, metasternum, abdominal ventrites, and legs unmodified; antennomeres IX and especially X shorter and less enlarged than male.

Collecting data: The only specimens known were collected in the "espinal", a pseudo-savanna with dominance of *Acacia*.

Distribution: *Achilia ovallensis* is known only from the Coquimbo Region (Limarí Province) of north-central Chile (Fig. 83: yellow stars).

Achilia frontalis Jeannel, 1962
Figs 27, 33, 37, 38-40, 45, 50, 71-76, 84

Achilia frontalis Jeannel, 1962: 409, 413 fig. 161 (aedeagus).
Achilia foveifrons Jeannel, 1962: 409, 414 fig. 165 (aedeagus) **syn. nov**.

Type material (8 ex.): CENTRAL CHILE: Región Los Lagos: Llanquihue prov.: MHNS; 1 ♂ (holotype of *Achilia foveifrons* n° 1777); Frutillar; 20.IX.1954; G. Kuschel. – MNHN; 1 ♂ and 1 ♀ (paratypes of *Achilia foveifrons*); Frutillar; 41° 08'S; 20.IX.1954; G. Kuschel. – Región Bío Bío: Ñuble prov.: MHNS; 1 ♂ (holotype of *Achilia frontalis* n° 1703); Chillàn; P. Germain. – MNHN; 1 ♂ and 3 ♀ (paratypes of *Achilia frontalis*); Chillàn; 36° 54'S; P. Germain.

Additional material (150 ex.): See Appendix 1.

Description: Body 1.35-1.55 mm long, generally bicolored with head, pronotum and abdomen blackish, elytra, antennae, and legs reddish, and palpi yellowish, or entirely reddish with darker abdomen, sometimes also entirely reddish with darker head. Head with eyes slightly longer than temples. Pronotum slightly wider than head, with maximal width on anterior half; median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae slightly diverging, extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.
Male: Head as in Figs 71-74; on each side with deep lateral pit with outer edge forming small tooth at level of eyes (Fig. 75), the latter occasionally absent (Fig. 76); frontal protuberance very swollen at base and anteriorly flattened to vertexal sulcus. Antennae (Fig. 33) with scape and pedicel longer than wide; antennomeres III-VIII slightly transverse; antennomeres VII-VIII with mesal margin protruding; antennomeres IX-X strongly transverse, with mesal margin protruding; antennomere X wider than IX; antennomere XI elongate, longer than VII-X combined, bearing long and thin subbasal seta inserted in deep depression. Metasternum with ovoidal median impression, posterior edge of the impression pubescent. Legs with trochanters simple; all femora (Figs 38-40) strongly thickened and sinuate, particularly metafemora; protibiae (Fig. 45) distinctly thickened on distal half, bearing small subapical tooth; mesotibiae (Fig. 50) at middle slightly bulging and bearing tuft of short setae; medial edge of metatibiae (Fig. 37) densely pubescent on apical half and distinctly narrowed subapically. Abdominal tergites unmodified; first abdominal ventrite impressed at middle, remaining ventrites flattened at middle; ventrite I with median carina extending from posterior margin to posterior edge of median impression. Aedeagus (Fig. 27) 0.325-0.335 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial recurved sclerites strongly sclerotised basally and apically pointed. Parameres wide with long seta on poorly developed outer lobe; tips recurved posteriorly and bearing wide subapical seta.
Female: Similar to male except: head with occipital protuberance less developed and lacking lateral pits; antennomere XI shorter than VII-X combined; disc of pronotum less convex; metasternum, abdomen, and legs unmodified.

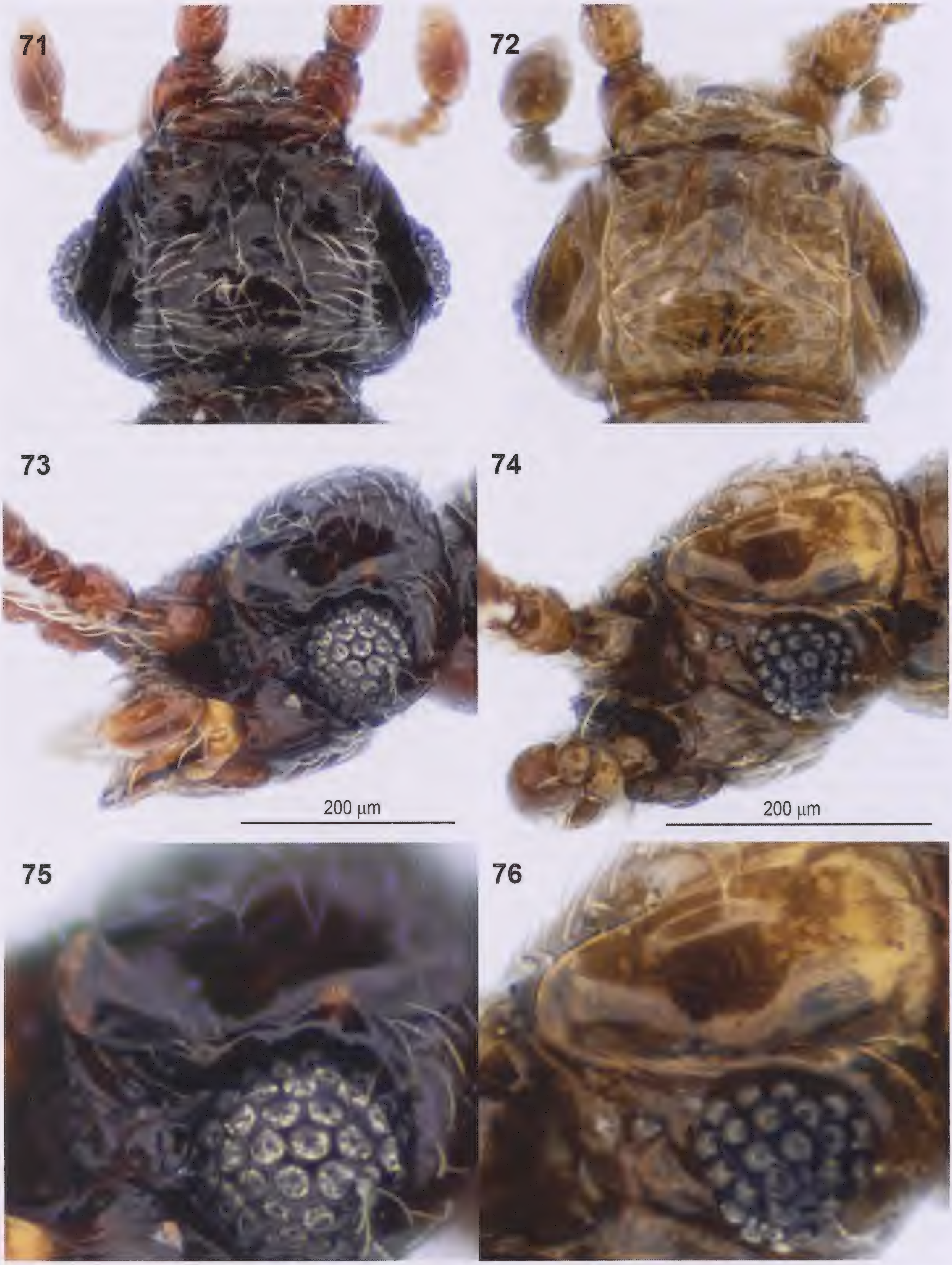
Collecting data: Collected from November to March, mainly in mixed forests at elevations ranging from 100 m to 700 m. Most specimens came from sifted samples of leaf and log litter, but some were also collected by flight intercept and carrion traps.

Distribution: *Achilia frontalis* is distributed in Central Chile from Chiloé to Ñuble Provinces (Fig. 84: blue triangles).

Comments: According to Jeannel (1962) the males of *A. foveifrons* differ from those of *A. frontalis* by their short and wide head for the anterior region (while being subtriangular in *A. frontalis*), the anterior part of the occipital protuberance occupying almost the entire width of the frons (while with a comparatively narrower vertex for *A. frontalis*), and the aedeagus with divergent dorsal longitudinal struts and thickened and sinuate copulatory pieces (while for *A. frontalis* the dorsal longitudinal struts are attached to each other, and the copulatory pieces are thin and not sinuate). However the aedeagal conformation of their types appear to be very similar, and after examination of extensive material it appears that these differences (when really present) have been strongly exaggerated by Jeannel and fall, in our opinion, within the intraspecific variation of this taxon. Therefore we conclude that *A. foveifrons* Jeannel, 1962 must be considered to be the junior synonym of *A. frontalis* Jeannel, 1962 (**syn. nov.**).

Achilia trauco n. sp.
Figs 28, 36, 46, 51, 77, 79, 84

Type material (75 ex.): CENTRAL CHILE: Región Los Ríos: Ranco prov.: MHNG; 1 ♂ (holotype); 34 km WNW La Union, station 36; 700 m; 17.XII.1984; S. & J. Peck; litter mixed evergreen forest. – Región Los Lagos: Osorno prov.: FMNH (FMHD #96-249); 1 ♂ and 1 ♀ (paratypes); 15.1 km W Puaucho; 40° 34.97'S 73° 37.68'W; 50 m; 30.XII.1996; A. Newton & M. Thayer 984; valdivian rainforest remnant in sm. ravine, w/large ferns, berlese, leaf & log litter. – Región Los Ríos: Ranco prov.: MHNG; 16 ♂ and 12 ♀ (paratypes); 34 km WNW La Union, station 36; 700 m; 17.XII.1984; S. & J. Peck; litter mixed evergreen forest. - MNHS; 1 ♂ and 1 ♀ (paratypes); same data; S. & J. Peck; litter mixed evergreen forest. – FMNH (FMHD #85-921, #85-36); 1 ♂ and 4 ♀ (paratypes); same data; S. & J. Peck. – MHNG; 12 ♂ and 1 ♀ (paratypes); 35 km WNW La Union; 700 m; 07.II.1985; S. & J.



Figs 71-76. *Achilia frontalis*. (71, 73, 75) specimen from Chillàn. (72, 74, 76) specimen from Frutillar. Male heads in dorsal (71-72) and lateral (73-74) views. (75-76) male supraocular area in lateral view. Scale bar left for (71, 73) and right for (72, 74).

Figs 77-82. (77, 79) *Achilia trauco*. (78, 80-82) *A. longispina*. Male head in (77-78) dorsal, (79-80) lateral and (81) dorso-posterior views. (82) male eye in frontal view. Scale bar left for (77, 79) and right for (78, 80-81).

Fig. 83. Distribution map. (● red circles) *Achilia excisa*. (▲ blue triangles) *A. pachycera*. (◆ green diamonds) *A. fiura*. (■ pink squares) *A. auriculata*. (✳ yellow stars) *A. ovallensis*.

Fig. 84. Distribution map. (● red circles) *Achilia testacea*. (▲ blue triangles) *A. frontalis*. (◆ green diamonds) *A. caracolana*. (■ pink squares) *A. trauco*. (✳ yellow stars) *A. longispina*.

Peck; litter mixed forest. – FMNH (FMHD #85-997, #85-36); 1 ♂ and 1 ♀ (paratypes); same data; S. & J. Peck; litter mixed forest. – Región Araucanía: Malleco prov.: FMNH (FMHD #85-1001, #85-118); 1 ♂ and 9 ♀ (paratypes); Purén, Contulmo Natural Monument; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter, berlese. – MHNG; 1 ♂ and 7 ♀ (paratypes); same data; S. & J. Peck. – Región Bío Bío: Arauco prov.: FMNH; 1 ♂ and 5 ♀ (paratypes); 16 km N Tres Pinos; 170 m; 12.XII.1982; A. Newton & M. Thayer; *Cupressus*, *Eucalyptus* etc. forest, berlese, leaf & log litter, forest floor.

Description: Body 1.15-1.4 mm long, generally bicolored with head, pronotum and abdomen blackish; elytra, antennae, and legs reddish, and palpi yellowish. Head with eyes longer than temples. Pronotum wider than head, with maximal width on anterior half and median antebasal fovea as large as lateral ones. First abdominal tergite with basal striae slightly diverging, extending to about one-third of paratergal length, and separated at base by about one-third of tergal width.
Head as in Figs 77 and 79; flanked by two deep lateral pits anteriorly at eyes, the upper margin of eyes surmounted by large carina; frontal protuberance very swollen. Antennae as in *A. frontalis*. Metasternum with deep ovoidal median depression; posterior edge of the depression pubescent. Legs with trochanters simple; all femora (Fig. 36) thickened and sinuate, particularly metafemora; protibiae (Fig. 46) slightly thickened on distal half; mesotibiae (Fig. 51) at middle slightly bulging and bearing tuft of short setae; medial edge of metatibiae densely pubescent on apical half and distinctly narrowed subapically. Abdominal tergites unmodified; first abdominal ventrite impressed at middle, remaining ventrites flattened at middle; ventrite I with median carina extending from posterior margin to posterior edge of median impression. Aedeagus (Fig. 28) 0.23-0.27 mm long; similar to that of *A. frontalis*, differing only by copulatory pieces being sinuate and subapically narrowed. Parameres wide with long seta on poorly developed outer lobe; tips recurved posteriorly and bearing thin and long subapical seta.
Female: Similar to male except: head with occipital protuberance less developed and lacking lateral pits; eyes less developed; disc of pronotum less convex; metasternum, abdomen, and legs unmodified.

Collecting data: Collected from December to February, mainly in mixed evergreen forests at elevations ranging from 50 m to 700 m. The specimens came from sifted samples of leaf and log litter.

Distribution: *Achilia trauco* n. sp. is distributed in Central Chile from Osorno to Arauco Provinces (Fig. 84: pink squares).

Comments: *Achilia trauco* n. sp. is very similar to *A. frontalis*, from which it differs mainly by the male features of head (see Figs 71-76, 77, 79), of the metafemora (see Figs 37-40, 36), the protibiae (see Figs 45 and 46), the mesotibiae (see Figs 50, 51), and the aedeagi (see Figs 27, 28). The females of *A. frontalis* and *A. trauco* n. sp. are very similar, except that those of *A. trauco* n. sp. have a slightly longer head, with a frontal protuberance more convex than those of *A. frontalis*.

Achilia longispina Franz, 1996

Figs 29, 34, 43, 52, 78, 80-82, 84

Achilia longispina Franz, 1996: 116 fig. 65 (aedeagus).

Type material (1 ex.): CENTRAL CHILE: Región Valparaíso: Valparaíso prov.: NHMW (coll. Franz); 1 ♂ (holotype); Mina de la Disputada (now Mina los Bronces), Anden bei Santiago de Chile; 3000-3400 m; 19.XI.1968; H. Franz.

Additional material (12 ex.): See Appendix 1.

Description: Body 1.6-1.7 mm long, entirely reddish or reddish brown, with palpi yellowish. Pubescence decumbent with long setae uniform on entire body. Head wider than long; lacking vertexal sulcus; eyes protruding and slightly pointed, longer than convex temples. Pronotum slightly wider than long, narrower than head, with maximal width at midlength; lateral outlines on anterior portion convergent, on posterior portion subparallel and sinuate; disc slightly convex, smooth and shiny with some punctures; basal margin bordered with row of contiguous shallow impressions; median antebasal fovea smaller than lateral ones. Elytra together wider than long with slightly protruding humeri; disc smooth, shiny, with two big basal foveae; sutural stria entire; discal stria extending to about elytral midlength. Legs elongate. Abdomen smooth, with some minute punctures; tergite I with basal striae slightly divergent, extending to about one-quarter of paratergal length, separated at base by more than one-third of tergal width, with some short and sparse setal brushes between striae.
Male: Head as in Figs 78 & 80-81, with deep lateral pits on each side of eyes, the latter with small median spine on upper margin (Fig. 82); frontal protuberance very large, raised, and flattened, densely covered with large punctures; clypeal area deeply hollowed laterally. Antennae (Fig. 34) with scape and pedicel distinctly longer than wide; antennomeres III-IV as long as wide; antennomeres V-VI longer than wide; antennomere VII as long as wide; antennomere VIII slightly wider than long; antennomere IX wider that long, with protruding mesal margin pointed in middle; antennomere X wider than long, wider and longer than IX, with protruding mesal margin indented and bearing numerous setae; antennomere XI longer than wide, narrower than X and longer than VIII-X combined, its surface bearing small tubercles. Metasternum with deep and broad

ovoidal median impression, posterior edge of impression pubescent. Legs with ventral margin of mesotrochanters (Fig. 43) bearing short seta; profemora and mesofemora slightly thickened, finely punctured; protibiae slightly thickened; mesotibiae (Fig. 52) in middle slightly bulging and bearing tuft of short setae; metatibiae slightly thickened and sinuate on basal third. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 29) 0.26-0.27 mm long; dorsal plate ovoid with dorsal longitudinal struts divergent; copulatory pieces consisting of pair of long medial sclerites basally recurved and sclerotised and apically pointed, associated on each side with small subapical sclerite. Parameres very wide with very long seta on well-developed outer lobe; tips strongly recurved posteriorly and bearing wide and long subapical seta.
Female: Similar to male except: head, metasternum, and legs unmodified; antennomeres X-XI shorter and thinner than male.

Distribution: *Achilia longispina* is known only from its type locality: Mina de la Disputada (now Mina los Bronces) in Central Chile, Valparaíso Province (Fig. 84: yellow stars).

Comments: The external morphology and aedeagal features of *A. longispina* resemble more closely *A. cribratifrons* Jeannel, 1962 and *A. angulifrons* Jeannel, 1963 than *A. frontalis*, as stated by Franz (1996: 116). Therefore we here exclude *A. longispina* from the *A. frontalis* group, but at this stage of the revision of the genus we prefer not to assign it to another group.

Achilia validicorniformis Franz, 1996

Achilia validicornisformis Franz, 1996: 117 fig. 66 (aedeagus).

Type material (17 ex.): CENTRAL CHILE: Región Los Lagos: Chiloé prov.: NHMW (coll. Franz); 1 ♂ (holotype); Chiloé Island, Chepu; 20.II.1990; T. Cekalovic. – NHMW (coll. Franz); 5 ♂ (4 without label of locality) and 11 ♀ (10 without label of locality) (paratypes); same data; T. Cekalovic.

Comments: We have examined the types of this species and found that all the specimens (holotype and paratypes) belong without doubt to *Achilia larvata* (Reitter, 1885), one of the species we recently revised (Sabella *et al.*, 2017). Therefore we here place *Achilia validicorniformis* Franz, 1996 as a junior synonym of *A. larvata* (Reitter, 1885) (**syn. nov.**).

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REFERENCES

Chandler D.S. 2001. Biology, Morphology, and Systematics of the Ant-like Litter Beetle Genera of Australia (Coleoptera: Staphylinidae: Pselaphinae). *Memoirs on Entomology, International* 15: i-viii, 1-560.

Franz H. 1996. Neue Beiträge zur Kenntnis der Pselaphidenfauna von Chile und Argentinien (Coleoptera: Pselaphidae). *Koleopterologische Rundschau* 66: 83-146.

Jeannel R. 1962. Les Psélaphides de la Paléantarctide Occidentale [pp. 295-479]. *In:* Debouttevi1le C.D. & Rapoport E. (eds.), Biologie de l'Amérique Australe. Vol. I. Etude sur la Faune du Sol. *Centre National de la Recherche Scientifique, Paris.*

Jeannel R. 1963. Les Psélaphides de la Paléantarctide Occidentale. Supplement [pp. 351-369]. *In:* Debouttevi1le C. D. & Rapoport E. (eds), Biologie de l'Amérique australe. Vol. II, Etudes sur la faune du sol. *Centre National de la Recherche Scientifique, Paris.*

Jeannel R. 1964. Sur quelques Psélaphides du Chili. *Revue Française d'Entomologie* 31: 5-12.

Kurbatov S. A., Sabella G. 2015. A revision of the Chilean Brachyglutini. Part 1. Some taxonomic changes in Brachyglutini and preliminary diagnosis of *Achilia* Reitter, 1890 (Coleoptera: Staphylinidae: Pselaphinae). *Revue suisse de Zoologie* 122(2): 297-306.

Reitter E. 1885. Beitrag zur Kenntniss der Pselaphiden-Fauna von Valdivia, Zweiter Theil. *Deutsche Entomologische Zeitschrift* 29: 321-332, pl. II.

Reitter E. 1890. Coleopterologische Notizen. XXXVIII. *Wiener Entomologische Zeitung* 9: 210-213.

Sabella G., Kurbatov S. A., Cuccodoro G. 2017. A revision of the Chilean Brachyglutini – Part 2. Revision of *Achilia* Reitter, 1890: *A. crassicornis, A. tumidifrons, A. bifossifrons* and *A. lobifera* species group (Coleoptera: Staphylinidae: Pselaphinae). *Revue suisse de Zoologie* 124(1): 119-140.

Schaufuss L. W. 1880 (1879). Beschreibung sechzig neuer Pselaphiden. *Nunquam Otiosus* 3: 481-511.

Appendix 1
Non-type material examined for the species mentioned in the Taxonomy section.

Achilia excisa (Schaufuss, 1880)
Additional material (1432 ex.): MNHN; 1 ♂; Chili. – CENTRAL CHILE: Región Los Lagos: Chiloé prov.: MHNG; 2 ♂; Chiloé, S-Chile; H. Franz. – MHNG; 27 ♂ and 105 ♀; Chiloé Island, Huillinco Lake; 31.I.1983; T. Cekalovic. – DBUC; 2 ♂ and 2 ♀; same data; T. Cekalovic. – MSNG; 4 ♂ and 6 ♀; same locality; TC-279; 22.II.1991; T. Cekalovic; ex *Chusquea* sp. – MSNG; 4 ♂ and 6 ♀; Chiloé Island, Huillinco Lake; TC-279; 22.II.1991; T. Cekalovic; ex *Chusquea* sp. – FMNH; 1 ♂; Chiloé Island, 1 km W Huillinco; TC-564; 24.I.1988; T. Cekalovic; berlese. – MSNG; 23 ♂ and 28 ♀;

same data; T. Cekalovic. – MHNG; 20 ♂ and 38 ♀; Chiloé Island, Piruquina; 26.II.1983; T. Cekalovic. – DBUC; 1 ♂ and 1 ♀; same data; T. Cekalovic. – MHNG; 1 ♂; Chiloé Island, 8 km Ancud, station 110; 01.II.1985; S. & J. Peck; forest remnants litter. – MHNG; 1 ♂; Chiloé Island, Río Pudeto; 28.II.1972; T. Cekalovic. – MHNG; 2 ♂; Chiloé Island, Castro; 17.II.1983; T. Cekalovic. – MHNG 1 ♂ and 1 ♀; Chiloé Island, Mocopulli; 02.II.1983; T. Cekalovic. – MHNS; 1 ♀ (paratype n° 1630 of *A. tumidifrons*); Chepu; 15.X.1958; G. Kuschel. – MHNS; 1 ♀ (as *A. tumidifrons*); Chepu; 17.X.1958; G. Kuschel. – MSNG; 2 ♂; Chiloé Island, Chepu; TC-580; 09.II.1999; T. Cekalovic. – MSNG; 3 ♂; same locality; TC-610; 20.I.2010; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-625; 26.I.2010; T. Cekalovic. – MNHN; 1 ♂ and 10 ♀; Chiloé Island, Chepu; 42° 03'S; 02.X.1958; G. Kuschel. – MNHN; 1 ♂ and 2 ♀; same locality; 03.X.1958; G. Kuschel. – MNHN; 2 ♂ and 3 ♀; same locality; 04.X.1958; G. Kuschel. – MNHN; 1 ♂; same locality; 07.X.1958; G. Kuschel. – MNHN; 3 ♀; same locality; 15.X.1958; G. Kuschel. – MNHN; 1 ♂ and 1 ♀; same locality; 16.X.1958; G. Kuschel. – MNHN; 6 ♂ and 17 ♀; same locality; 17.X.1958; G. Kuschel. – MNHN; 1 ♂; Cerros de San Pedro; 42° 20'S; 08.XI.1958; G. Kuschel. – MHNG; 1 ♀; Quinchao Island, Curaco de Veles; 30.I.1983; T. Cekalovic. – MSNG; 1 ♂; Chiloé Island, Estero Tablin; TC-609; 19.I.2000; T. Cekalovic. – MSNG; 2 ♂; Chiloé Island, San Juan de Chadmo; TC-555; 18.I.1998; T. Cekalovic. – MSNG; 2 ♂; Chiloé Island, Puente La Caldera; TC-466; 15.II.1996, T. Cekalovic. – FMNH (FMHD# 97-21); 1 ♂ and 1 ♀; Puente La Caldera, 9.8 km E of Cucao; 42° 39.96'S 74° 00.70'W; 10 m; 14.I.1997; A. Newton & M. Thayer 991; valdivian rainforest, berlese, leaf & log litter. – MSNG; 1 ♂; Chiloé Island, 1 km N of Puente Notuco; TC-528; 20.II.1997; T. Cekalovic. – MSNG; 9 ♂ and 20 ♀; Chiloé Island, Puente Milildeo; TC-471; 15.II.1995; T. Cekalovic. – DBUC; 2 ♂ and 4 ♀; same data; T. Cekalovic. – MSNG; 6 ♂ and 10 ♀; Chiloé Island, 5 km SW Chonchi; TC-560; 21.I.1998; T. Cekalovic. – MSNG; 6 ♂ and 5 ♀; Quinchao Island, Quetro; TC-559; 20.I.1998; T. Cekalovic. – MSNG; 5 ♂ and 8 ♀; same locality; TC-582; 12.II.1999; T. Cekalovic. – MSNG; 3 ♂ and 5 ♀; Quinchao Island, Laguna Pulul; TC-615; 22.I.2000; T. Cekalovic. – FMNH (FMHD #97-22); 3 ♂ and 7 ♀; SE edge of Lago Tepuhueico; 42°48.11'S 73°55.36'S; 50 m; 15.I.1997; valdivian rainforest; A. Newton & M. Thayer 992; berlese, leaf & log litter. – Llanquihue prov.: MHNG; 1 ♂; Petrohué; 30.I.1979; A. De Chambrier. – UNHC; 2 ♂; Saltos Petrohué, 6.4 km SW Petrohué; 140 m; 28.XII.1982; A. Newton & M. Thayer; valdivian rainforest, forest floor. – FMNH (FMHD #97-8); 6 ♂; Vicente Perez Rosales National Park, 9.2 km NE Ensenada, on road to Petrohué; 41° 10.20'S 72° 27.10'W; 125 m; 02-28.I.1997; A. Newton & M. Thayer 987; valdivian rainforest w/ *Nothofagus* ssp., flight intercept trap. – FMNH (FMHD #97-10); 3 ♀; same locality; 02.I.1997; A. Newton & M. Thayer 987; valdivian rainforest w/ *Nothofagus* ssp., berlese, leaf & log litter. – FMNH (FMHD #97-11); 1 ♂; Vicente Perez Rosales National Park, SW slope Volcan Osorno, km 10.1 to La Burbuja; 41° 08.30'S 72° 32.15'W; 925 m; 03-27.I.1997; A. Newton & M. Thayer 988; *Nothofagus dombeyi* & *Podocarpus nubigena* w/valdivian rainforest understory, flight intercept trap. – FMNH (FMHD #97-16); 34 ♂ and 23 ♀; Lago Chapo, near SE end, km 9.9 on road from Rollizo; 41° 30.63'S 72° 23.98'W; 385 m; 04.I.1997; A. Newton & M. Thayer 989; valdivian rainforest on steep slope, berlese, leaf & log litter. – FMNH (FMHD #97-14); 4 ♂; same locality; 04-26.I.1997; A. Newton & M. Thayer 989; valdivian rainforest on steep slope, intercept traps. – MNHN; 3 ♂ and 7 ♀; Frutillar; 41° 08'S; 20.IX.1957; G. Kuschel. – MNHN; 5 ♂ and 5 ♀; Los Riscos; 41° 13'S; 11.IV.1954; G. Kuschel. – Osorno prov.: FMNH; 20 ♂ and 10 ♀; Puyehue National Park, Antillanca road; 470 m; 20-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, Berlese, leaf & log litter, forest floor. – FMNH; 6 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor, voucher associated with larvae. – UNHC; 4 ♂; same data; A. Newton & M. Thayer – MHNG; 2 ♂; Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – FMNH (FMHD #85-996, #85-113) 1 ♂; Puyehue National Park, Anticura Repucura trail; 500 m; 06.II.1985; S. & J. Peck; forest litter. – MNHG; 15 ♂ and 15 ♀; same data; S. & J. Peck. – FMNH; 30 ♂ and 52 ♀; Puyehue National Park, 4.1 km E Anticura, trap site 662; 430 m; 19-26.XII.1982; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae, berlese, leaf & log litter, forest floor. – UNHC; 12 ♂ and 1 ♀; same data; A. Newton & M. Thayer. – FMNH; 4 ♂; same data; A. Newton & M. Thayer; valdivian rainforest, window trap 662. – FMNH (FMHD# 96-250); 17 ♂ and 2 ♀; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.XII.1996/30.I.1997; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothaea,* flight intercept trap. – FMNH (FMHD #97-41); 12 ♂ and 14 ♀; same locality; 30.I.1997; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothaea*, berlese, leaf and log litter. – FMNH (FMHD #97-40); 23 ♂ and 17 ♀; same data; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothaea*, berlese, leaf and log litter. – FMNH (FMHD# 97-39); 24 ♂ and 39 ♀; same data; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothaea* berlese, leaf & log litter. – FMNH (FMHD #97-4); 10 ♂ and 2 ♀; same locality; 01-30.I.1997; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothaea,* flight intercept trap. – FMNH (FMHD# 97-5); 21 ♂; same locality; 01-30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothaea,* flight intercept trap. – FMNH (FMHD #2002-90); 11 ♂ and 20 ♀; Puyehue National Park, Ruta 215; km 4.5 of Aduana station; 40° 40.23'S 72° 05.21'W; 580 m; 19.XII.2002; A. Newton, M. Thayer, D. J. Clarke & M. Chani 1071; valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #85-933, #85-48); 1 ♂; 3 km S Maicolpué, Bahia Mansa; 200 m; 03. II.1985; S. & J. Peck. – MHNG; 8 ♂ and 3 ♀; same data; S. & J. Peck. – MHNG; 2 ♀; same locality; 21.XII.1984; S. & J. Peck. – FMNH (FMHD #96-247); 3 ♂ and 2 ♀; Hills S of Maicolpué; 40° 36.57'S 73° 44.91'W; 160 m; 30.XII.1996; A. Newton & M. Thayer 983; disturbed valdivian rainforest, berlese, leaf & log litter. – MHNG; 1 ♂; Pucatrihue, 65 km W Osorno, station 21; 40° 28'S 73° 43'W; 150 m; 04.XII.1984; D. Burckhardt; valdivian rainforest sifting of moss on dead tree trunks, branches and rocks an of vegetable detritus. – MHNG; 12 ♂ and 18 ♀; Puyehue National Park, Aguas Calientes; 500 m; 20.XII.1984; S. & J. Peck; forest litter on trail, sifting. – MHNG; 2 ♂; same locality; 20.XII.1984/08.II.1985; S. & J. Peck; FIT, derumbes forest trail. – MHNG; 32 ♂ and 48 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; M. Agosti & D. Burckhardt. – PHPC; 3 ♂ and 3 ♀; Puyehue National Park, near Termes Aguas Calientes, 26.2 km E Entre Lagos; 40° 44.130'S 72° 18.427'W; 460 m; 09-12.III.2008; H. Wood & C. Griswold. – FMNH (FMHD #96-244); 1 ♂; Puyehue National Park,

Antillanca road, 7.2 km above Aguas Calientes, 40° 45.55'S 72° 17.82'W; 660 m; 29.XII.1996/01.II.1997; A. Newton & M. Thayer 982; valdivian rainforest w/ *Saxegothaea* dominant, dense *Chusquea,* flight intercept trap. – MSNG; 2 ♂; Los Ñilques; TC-260; 13.I.1990; T. Cekalovic. – FMNH (FMHD #96-248); 1 ♂; 15.1 km W Puaucho; 40° 34.97'S 73° 37.68'W; 50 m; 30.XII.1996; A. Newton & M. Thayer 984; valdivian rainforest remnant in sm. ravine, w/large ferns, berlese, leaf & log litter. – UNHC; 1 ♂; 7.7 km NE Termas de Puyehue, site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor. – Región Los Ríos: Ranco prov: MSNG; 1 ♂; 8 km S of Pichirropulli; TC-261; 13.I.1990; T. Cekalovic. – FMNH (FMHD #85-921, #85-36); 1 ♀; 34 km WNW La Union, station 36; 700 m; 17.XII.1984; S. & J. Peck; litter mixed evergreen forest. – MHNG; 81 ♂ and 102 ♀; same data; S. & J. Peck. – FMNH (FMHD #85-997, 85-114); 2 ♂; 35 km WNW La Union; 700 m; 07.II.1985; S. & J. Peck; litter mixed forest. – MHNG; 2 ♂; same data; S. & J. Peck. – MHNG; 3 ♂; same locality; 17.XII.1984; S. & J. Peck; mixed evergreen forest. – MHNG; 8 ♂; 35 km WNW La Union; 700 m; 17.XII.1984/07.II.1985; S. & J. Peck; FIT, mixed evergreen forest. – FMNH; 3 ♂ and 1 ♀; 4.1 km W Anticura, site 663; 270 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flight intercept (windows) trap. – UNHC; 3 ♂ and 1 ♀; same data; A. Newton & M. Thayer. – FMNH; 3 ♂ and 4 ♀; same locality; A. Newton & M. Thayer; valdivian rainforest, voucher associated with larvae. – Valdivia prov.: MHNG; 2 ♀; Cordillera Valdivia (bajo tierra); 120 m; 04-09.III.1955; L. E. Peña. – PHPC; 1 ♂; Oncol Park, 12 km NW Valdivia, Sendero Bonifacio, WDS-T-201; 39° 42'S 73° 19'W; 22.II.2008; W. D. Shepard; sifting litter. – FMNH (FMHD #97-18); 2 ♂; Rincón de La Piedra, turnoff, 14.8 km SE Valdivia; 39° 55' 32"S 73° 06' 27"W; 50 m; 11.I–01.II.1997; A. Newton & M. Thayer 990; disturbed valdivian rainforest, with *Nothofagus dombeyi* and *Podocarpus saligna*, flight intercept (windows) trap. – FMNH (FMHD #97-20); 27 ♂ and 43 ♀; same locality; 11.I.1997; A. Newton & M. Thayer 958; disturbed valdivian rainforest, with *Nothofagus dombeyi* and *Podocarpus saligna*, berlese, leaf & log litter. – Región Araucanía: Cautín prov.: MHNG; 1 ♂; Caburgua Lake; 01.XII.1978; T. Cekalovic. – MHNG; 2 ♂; Huerquehue National Park, station 16a; 800-900 m; 22-24.XII.1980; M. Agosti & D. Burckhardt; forest litter. – MHNG; 2 ♂ and 1 ♀; Huerquehue National Park, station 17a; 800 m; 22-25.XII.1980; M. Agosti & D. Burckhardt; forest litter. – Malleco prov.: FMNH (FMHD #85-1001, #85-118); 3 ♂; Purén, Natural Monument Contulmo; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter, berlese. – FMNH (FMHD# 2002-64); 3 ♂ and 5 ♀; Natural Monument Contulmo, Sendero Lemu Mau; 38° 00.74'S 73° 11.13"W; 410 m; 08.XII.2002; D. J. Clarke & A. Solodovnikov 1059; *Nothofagus obliqua-Eucryphia cordifolia* w/fern & bamboo understory, sifted litter, hand-collected. – MHNG; 18 ♂ and 37 ♀; same data; S. & J. Peck. – UNHC; 4 ♂; 10 km W Purén, Natural Monument Contulmo; 240 m; 12.XII.1982; A. Newton & M. Thayer; mixed hdwd. forest with *Chusquea*, berlese, leaf & log litter, forest floor. – FMNH (FMHD #96-216); 1 ♂; Nahuelbuta National Park, Comallín, 8.2 km NW Los Portones entrance; area; 37° 48.21'S 73° 00.89'W; 1260 m; 21.XII.1996/07.II.1997; A. Newton & M. Thayer 974; *Nothofagus* ssp.-*Araucaria araucana* forest, flight intercept trap. – MNHN; 5 ♂ and 6 ♀; Mocha Island; 38° 20'S; 300 m; 12.X.1959; G. Kuschel. – MNHN; 1 ♀; same locality; 13.X.1959; G. Kuschel.

Achilia pachycera Jeannel, 1963

Additional material (150 ex.): CENTRAL CHILE: Región Araucanía: Malleco prov.: MNHN; 1 ♂; Nahuelbuta, N1W – MNHN; 1 ♂ and 1 ♀; Nahuelbuta, N3W – MNHN; 1 ♂ and 1 ♀; Nahuelbuta, N5W – MHNG; 1 ♂ and 1 ♀; Nahuelbuta National Park, station 30b; 37° 50'S 73° 00'W; 1100 m; 23.XII.1992; D. Burckhardt; sifting of moss on stone, dead wood and of vegetational debris in *Araucaria-Nothofagus dombeyi* forest along creak with river. – MHNG; 1 ♂; Nahuelbuta National Park, Piedra del Aquila, station 31b; 37° 48'S 73° 02'W; 1300 m; 24.XII.1992; D. Burckhardt; sifting of moss on rock and tree trunks and vegetational debris. – FMNH (FMHD #96-222); 2 ♂; Nahuelbuta National Park, 4.5 km W Los Portones entrance; 37° 49.25'S 72° 59.82'W; 1300 m; 21.XII.1996/07.II.1997; A. Newton & M. Thayer 975; *Nothofagus* ssp. emergent *Araucaria araucana, Chusquea* understory, flight intercept trap. – FMNH (FMHD #96-224); 59 ♂ and 81 ♀; same locality; 21.XII.1996; A. Newton & M. Thayer 975; *Nothofagus* ssp. emergent *Araucaria araucana, Chusquea* understory, berlese, leaf & log litter.

Achilia testacea Jeannel, 1962

Additional material (103 ex.): MNHN; 12 ♂ and 1 ♀; Chile. – CENTRAL CHILE: Región Los Lagos: Chiloé prov.: MHNG; 1 ♂; Chiloé, S-Chile; H. Franz. – MHNS; 1 ♀ (mislabeled as paratype of *Achilia testacea* n. 1691); Chiloé Island, Chepu; 15.X.1958; G. Kuschel. – MSNG; 2 ♂ and 3 ♀; same locality; TC-275; 19.II.1991; T. Cekalovic. – DBUC; 2 ♂ and 2 ♀; TC-275; same locality; 19.II.1991; T. Cekalovic. – MSNG; 1 ♀; same locality; TC-610; 20.I.2010; T. Cekalovic. – MHNG 1 ♂ and 1 ♀ ; Chiloé Island, Vilupulli; II.1993; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-563; 23.I.1998; T. Cekalovic. – MHNG; 1 ♂; Chiloé Island, Huillinco Lake; 31.I.1983; T. Cekalovic. – MSNG; 4 ♀; same locality; TC-279; 22.II.1991; T. Cekalovic; ex *Chusquea* sp. – MSNG; 2 ♀; Chiloé Island, 1 km W Huillinco; TC-564; 24.I.1988; T. Cekalovic; berlese. – MHNG; 2 ♂ and 1 ♀; Chiloé Island, Río Pudeto; 28.II.1972; T. Cekalovic. – MHNG; 2 ♂; same locality; 10.II.1981; T. Cekalovic. – MSNG; 1 ♂ and 1 ♀; same locality; SyTC-226; 21.II.1989; S. & T. Cekalovic. – FMNH (FMHD #2002-068); 1 ♀; Quemchi, 11 km W of (11 km E Hwy 5); 42° 10.40'S 73° 35.73'W; 140 m; 10.XII.2002; A. Solodovnikov & A. Newton 1060; valdivian rainforest remnant w/thick bamboo understory; berlese, leaf & log litter. – FMNH (FMHD #97-24); 4 ♀; Colonia Yungay road to (3.6 km W Hwy) 5; 42° 59'S 73° 41'W; 90 m; 17.I.1997; A. Newton & M. Thayer 995; grazed secondary valdivian rainforest remnants, berlese, leaf & log litter. – FMNH (FMHD #2002-78); 1 ♀; Colonia Yungay road to, ca 4 km NW Ruta 5; 42° 59.12'S 73° 42.02'W; 110-115 m; 13.XII.2002; A. Solodovnikov & M. Thayer 1064; disturbed valdivian rainforest w/recent selective cutting, berlese, leaf & log litter. – FMNH (FMHD #97-25); 1 ♂; Miraflores, road to (0.6 km W Hwy 5); 42°46.73'S 73°47.71'S; 130 m; 17.I.1997; secondary valdivian rainforest; A. Newton & M. Thayer 994; berlese, leaf & log litter. – MSNG; 1 ♂; Chiloé Island, Cruce a Alcaldeo; TC-281; 22.II.1991; T. Cekalovic. – MSNG; 2 ♂ and 3 ♀; Chiloé Island, 5 km SW Chonchi; TC-560; 21.I.1998; T. Cekalovic. – MSNG; 2 ♀; same locality; TC-623; 25.I.2000; T. Cekalovic. – MSNG; 2 ♀; Chiloé Island, Puente La Caldera; TC-466; 15.II.1996, T. Cekalovic. – MSNG; 1 ♂; Chiloé Island, 1 km N of Puente Notuco; TC-528; 20.II.1997; T. Cekalovic. – MSNG; 2 ♂ and 3 ♀; Quinchao Island, Quetro; TC-559; 20.I.1998; T. Cekalovic. – DBUC; 1 ♂ and 2 ♀; same locality; 20.I.1998;

T. Cekalovic. – MSNG; 2 ♂ and 1 ♀; same locality; TC-582; 12.II.1999; T. Cekalovic. – MSNG; 1 ♂; Quinchao Island, Laguna Pulul; TC-615; 22.I.2000; T. Cekalovic. – Llanquihue prov.: MNHN; 1 ♂ and 1 ♀; Frutillar; 41° 08'S; 20.IX.1954; G. Kuschel. – MHNS; 1 ♀ (mislabeled as paratype of *Achilia testacea* n. 1693); same data. – MNHN; 1 ♀; Los Riscos; 41° 13'S; 11.IV.1954; G. Kuschel. – FMNH (FMHD #85-947, #85-63); 1 ♂; Lenca, 45 km SE Puerto Montt; 100 m; 25.XII.1984; S. & J. Peck; forest remnant, leaf stick litter, berlese. – FMNH (FMHD #97-29); 1 ♂; Puerto Montt, 50 km SW on Hwy 5, 0.7 km NE jct. to Maullín; 41° 43.20'S 73° 22.27'W; 60 m; 20.I.1997; A. Newton & M. Thayer 999; secondary valdivian rainforest remnants, berlese, leaf & log litter. – MSNG; 3 ♂ and 3 ♀; Cruce Abtao; SyTC-227; 21.II.1989; S. & T. Cekalovic. – DBUC; 1 ♂ and 1 ♀; same locality; 21.II.1989; S. & T. Cekalovic. – MHNG; 1 ♀; La Arena, 45 km SE Puerto Montt; 100 m; 25.XII.1984; S. & J. Peck. – Osorno prov.: MHNG; 1 ♂; environs of Osorno, S-Chile; H. Franz. – MHNG; 7 ♂ and 3 ♀; 3 km S Maicolpué, Bahìa Mansa; 21.XII.1984; S. & J. Peck; mixed forest litter. – (FMHD #85-933, #85-48); 1 ♂; same locality; 21.XII.1984; S. & J. Peck; litter, mixed forest litter. – FMNH (FMHD #85-994, #85-111); 1 ♀; same locality; 200 m; 03.II.1985; S. & J. Peck; mixed forest litter. – FMNH (FMHD# 96-247); 5 ♂ and 1 ♀; Hills S of Maicolpué; 40° 36.57'S 73° 44.91'W; 160 m; 30.XII.1996; A. Newton & M. Thayer 983; disturbed valdivian rainforest, berlese, leaf & log litter. – UNHC; 1 ♂; 7.7 km NE Termas de Puyehue, site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor. – Región Los Ríos: Valdivia prov.: MSNG; 1 ♀; Lago Calafquen, 2 km N of Coñaripe; TC-434; 26.I.1995; T. Cekalovic. – Región Araucanía: Cautín prov.: FMNH; 1 ♀; Bellavista, North shore Lago Villarica, site 655; 310 m; 15-30.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flood debris forest stream. – FMNH; 1 ♂; Puente Pedregoso; 06.XII.1992; T. Cekalovic. – Región Bío Bío: Bío Bío prov.: MNHN; 1 ♀; Abanico; 37° 23'S; 17.V.1957; G. Kuschel. – Ñuble prov.: MHNS; 1 ♂ and 2 ♀ (mislabelled as paratypes of *Achilia frontalis* n° 1765, 1730 and 1741); – Chillàn; P. Germain. – MNHN; 4 ♀; Chillàn; P. Germain. – MHNG; 4 ♂; near Recinto, about 60 km E Chillàn, station 7a; 400-450 m; 12.XII.1990; M. Agosti & D. Burckhardt; forest litter. – MSNG; 1 ♀; Los Llohue; TC-299; 07.XII.1991; T. Cekalovic.

Achilia caracolana Jeannel, 1962
Additional material (318 ex.): CENTRAL CHILE: Región Los Lagos: Chiloé prov.: MHNG; 1 ♂; Chiloé Island, Piruquina; 26.II.1976; T. Cekalovic. – Región Araucanía: Cautín prov.: FMNH; 1 ♂ and 19 ♀; Ñielol National Park, near Temuco, site 652; about 250 m; 14-30.XII.1982; A. Newton & M. Thayer; native forest remnants with *Nothofagus*, vouchers associated with larvae, leaf & log litter, forest floor. – UNHC; 1 ♂; same data; A. Newton & M. Thayer. – Región Bío Bío: Arauco prov.: FMNH; 1 ♂; 16 km N Tres Pinos; 170 m; 12.XII.1982; A. Newton & M. Thayer; *Cupressus*, *Eucalyptus* etc. forest, berlese, leaf & log litter, forest floor. – Bío Bío prov.: MHNG; 1 ♂; Saltos del Laja, N of Los Angeles; H. Franz. – Concepción prov.: MHNS; 2 ♀ (mislabeled as paratypes of *Achilia caracolana* n° 1687-1688); Cerro Caracol; 24.V.1957; G. Kuschel. – MHNG; 1 ♀; same locality; 25.III.1977; T. Cekalovic. – FMNH; 11 ♀; same locality; TC-290; 14.IX.1991; T. Cekalovic – MSNG; 2 ♂ and 17 ♀; same locality; TC-297; 04.XII.1991, T. Cekalovic; *Chusquea* sp. – MSNG; 2 ♀; same locality; TC-298; 04.XII.1991, T. Cekalovic; ex *Peumus boldus* – FMNH; 1 ♂ and 14 ♀; same locality; TC-367; 17.XI.1993; T. Cekalovic. – DBUC; 3 ♂; same data; T. Cekalovic. – MSNG; 1 ♂ and 6 ♀; same locality; TC-484; 07.IX.1996; T. Cekalovic. – MSNG; 1 ♂ and 8 ♀; same locality; TC-506; 05.XII.1996, T. Cekalovic. – FMNH; 4 ♂ and 54 ♀; Cerro Caracol, Mirador Alemán; TC-368; 28.XI.1993; T. Cekalovic. – DBUC; 12 ♀; same data; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-402; 28.III.1994; T. Cekalovic. – FMNH; 1 ♂; Nonguén; 25.IX.1976; T. Cekalovic. – FMNH; 1 ♂; Camino de Lirquen a Tomé; 10.VIII.1968; T. Cekalovic. – MHNG; 2 ♂ and 17 ♀; Concepción; 09.IV.1977; T. Cekalovic. – DBUC; 2 ♂ and 1 ♀; same data; T. Cekalovic. – MHNG; 4 ♂ and 19 ♀; Hualpén; 05.III.1977; T. Cekalovic. – DBUC; 1 ♂ and 1 ♀; same data; T. Cekalovic. – MHNG; 1 ♂; same locality; 09.III.1977; T. Cekalovic. – MHNG; 2 ♂ and 2 ♀; same locality; 01.I.1979; T. Cekalovic. – MHNG; 1 ♂; Pinares; 18.III.1973; T. Cekalovic. – MSNG; 11 ♂ and 13 ♀; Escuadron; TC-205; 03.IV.1988; T. Cekalovic; bajo *Chusquea* sp. – DBUC; 2 ♂ and 4 ♀; same data; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-204; 02.IV.1988; T. Cekalovic; ex *Peumus boldus*. – MSNG; 3 ♂ and 3 ♀; same locality; TC-207; 16.IV.1988, T. Cekalovic. – MSNG; 1 ♂; Caleta Chome; TC-291; 21.IX.1991; T. Cekalovic. – MSNG; 1 ♂ and 2 ♀; same locality; TC-295; 30.XI.1991; T. Cekalovic; ex. *Peumus boldus*. – MSNG; 1 ♂; same locality; TC-511; 01.I.1997; T. Cekalovic. – MSNG; 1 ♂; Rocoto; 15.VI.1986; T. Cekalovic. – MSNG; 5 ♂ and 12 ♀; same locality; TC-294; 16.XI.1991; T. Cekalovic. – MSNG; 4 ♂ and 4 ♀; same locality; TC-26; 01.I.1971; T. Cekalovic. – MSNG; 19 ♀; Las Escaleras; TC-242; 24.IX.1989; T. Cekalovic. – MSNG; 2 ♂ and 3 ♀; same locality; TC-255; 05.XII.1989; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-420; 04.I.1995; T. Cekalovic. – MSNG; 1 ♂; Collico; TC-188; 29.XII.1987; T. Cekalovic. – MSNG; 5 ♂ and 4 ♀; Lagunillas; TC-206; 10.IV.1988; T. Cekalovic. – MSNG; 1 ♂; Peniquillo; TC-516; 30.I.1997; T. Cekalovic. – Región Maule: Cauquenes prov.: FMNH (FMHD #81-146); 1 ♂; W of Cauquenes, Cayurranquil; 500 m; 23.I.1981; L. E. Peña; *Nothofagus glauca* litter. – Talca prov.: FMNH (FMHD #96-208); 1 ♀; Area de Protección Vilches, Piedras Tacitas area; 35° 36.53'S 71° 04.10'W; 1185 m; 17.XII.1996; A. Newton & M. Thayer 101; *Nothofagus* ssp. with shrubs along stream, berlese, leaf & log litter.

Achilia auriculata Jeannel, 1962
Additional material (4 ex.): CENTRAL CHILE: Región Bío Bío: Concepción prov.: MSNG; 1 ♂; Peniquillo; TC-311; 15.IX.1992; T. Cekalovic. – MHNG; 1 ♂; same data. – UNHC; 1 ♂ (only aedeagus) and 1 ♀; 8.4 km W of La Florida; 170 m; 02.I.1983; A. Newton & M. Thayer; subtropical xerophytic forest, berlese, leaf & log litter, forest floor. – FMNH; 1 ♀; Florida; 03.X.1977; T. Cekalovic.

Achilia ovallensis Jeannel, 1962
Additional material (3 ex.): CENTRAL-NORTHERN CHILE: Región Coquimbo: Limarí prov: MHNS; 3 ♀ (mislabelled as paratypes of *Achilia ovallensis* n° 1697-98, 1700); Ovalle; P. Germain.

Achilia frontalis Jeannel, 1962
Additional material (150 ex.): CENTRAL CHILE: Región Los Lagos: Chiloé prov.: MSNG; 4 ♂; Rio Pudeto; SyTC-226; 21.II.1989, S. & T. Cekalovic. – Llanquihue prov.: MNHN; 3 ♀ (as *A. bicornis*); Frutillar; 20.IX.1954; G. Kuschel. – MSNG;

1 ♂ and 9 ♀; Frutillar; TC-283; 23.II.1991; T. Cekalovic. – MHNG; 1 ♂; Frutillar Bajo, Universidad Chile Forest Reserve; 100 m; 22.XII.1984/02.II.1985; S. & J. Peck; FIT ravine mixed forest. – Osorno prov.: MHNG; 7 ♂ and 1 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; M. Agosti & D. Burckhardt. – DBUC; 1 ♂; same data; M. Agosti & D. Burckhardt. – PHPC; 1 ♂ and 1 ♀; Puyehue National Park, near Termes Aguas Calientes, 26.2 km E Entre Lagos; 40° 44.130'S 72° 18.427'W; 460 m; 09-12. III.2008; H. Wood & C. Griswold. – FMNH (FMHD #85-928, #85-43); 1 ♂; Puyehue National Park, Aguas Calientes; 500 m; 20.XII.1984; S. & J. Peck; forest litter on trail, sifting. – UNHC; 1 ♂; Puyehue National Park, Antillanca road; 470 m; 20-25. XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor. – FMNH; 2 ♂ and 1 ♀; same data; A. Newton & M. Thayer. – DBUC; 2 ♂; same data; A. Newton & M. Thayer. – MSNG; 1 ♂; Los Ñilques; TC-260; 13.I.1990; T. Cekalovic. – Región Los Ríos: Ranco prov.: FMNH (FMHD #57-124); 1 ♀; Río Gol-Gol; 09-13.XI.1957; L. Peña; forest. – MHNG; 6 ♂ and 4 ♀; 34 km WNW La Union, station 36; 700 m; 17.XII.1984 S. & J. Peck; litter mixed evergreen forest. – FMNH (FMHD #85-921, #85-36); 1 ♂; same data; S. & J. Peck; litter mixed evergreen forest. – Valdivia prov.: PHPC; 1 ♂; 12 km NW Valdivia; WDST-201; 39° 42'S 73° 19'W; 21-22.II.2008; William D. Shepard; sifting litter. – Región Araucanía: Cautín prov.: MHNG; 1 ♂ and 6 ♀; Ñielol National Park, Temuco, site 652; 300 m; 13.XII.1984; S. & J. Peck; mixed evergreen forest. – UNHC; 3 ♂; same locality; about 250 m; 14-30.XII.1982; S. & J. Peck; native forest remnants w/ *Nothofagus* berlese, leaf & log litter, forest floor. – FMNH; 5 ♂ and 9 ♀; same data; S. & J. Peck. – DBUC; 3 ♀; same data; S. & J. Peck. – Malleco prov.: FMNH; 8 ♂ and 10 ♀; Contulmo National Park, 10 km W Purén; 240 m; 12.XII.1982; A. Newton & M. Thayer; mixed hdwd. forest with *Chusquea*, berlese, leaf & log litter, forest floor. – DBUC; 3 ♂ and 6 ♀; same data; A. Newton & M. Thayer. – UNHC; 3 ♂; same data; A. Newton & M. Thayer. – FMNH (FMHD #85-1001, #85-118); 3 ♂ and 5 ♀; Purén, Contulmo Natural Monument; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter, berlese. – DBUC; 1 ♂; same data; S. & J. Peck; mixed forest litter, berlese. – FMNH (FMHD #85-904, #85-18); 1 ♀; same locality; 11.II.1984/13.II./1985; S. & J. Peck; mixed evergreen forest, carrion trap. – MHNG; 23 ♂ and 36 ♀; same locality; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter, berlese. – DBUC; 1 ♂ and 1 ♀; same data; S. & J. Peck. – FMNH (FMHD# 2002-64); 2 ♂ and 7 ♀; Contulmo Natural Monument, Sendero Lemu Mau; 38° 00.74'S 73° 11.13"W; 410 m; 08.XII.2002; A. Newton & A. Solodovnikov 1059; *Nothofagus obliqua-Eucryphia cordifolia* w/fern & bamboo understory, sifted litter, hand-collected. – Región Bío Bío: Arauco prov.: MHNG; 1 ♂; Cordillera of Nahuelbuta; 18.III.1966; T. Cekalovic. – Bío Bío prov.: MNHN; 3 ♂ and 1 ♀; Pemehue; 38° 00'S; 1896; P. Germain. – MNHN; 1 ♀; Pemehue; P. Germain. – Concepción prov.: MHNG; 1 ♂ and 3 ♀; Pinares; 17.II.1979; T. Cekalovic. – MSNG; 1 ♂ and 6 ♀; Estero Nonguén; TC-544; 20.I.1997; T. Cekalovic. – Ñuble prov.: MHNG; 2 ♂ and 7 ♀; near Recinto, about 60 km E Chillàn, station 7a; 400-450 m; 12.XII.1990; M. Agosti & D. Burckhardt; forest litter. – MHNS; 3 ♀ (mislabelled as paratypes of *Achilia testacea* n. 1705, 1749 and 1758); Chillàn; P. Germain. – Región Valparaíso: Valparaíso prov.: MNHN; 1 ♀; Quillota.

Achilia longispina Franz, 1996

Additional material (12 ex.): CENTRAL CHILE: Región Valparaíso: Valparaíso prov.: NHMW (coll. Franz); 2 ♂ and 9 ♀; Mina de la Disputada (now Mina los Bronces), Anden bei Santiago de Chile; 3000-3400 m; 19.XI.1968; H. Franz. – MHNG; 1 ♂; same data; H. Franz.

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Subterranean *Neobisium* (Pseudoscorpiones: Neobisiidae) from Albania

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Abstract: Two new subterranean pseudoscorpion species are described from caves of northern Albania: *Neobisium (Blothrus) latellai* n. sp. and *Neobisium (Blothrus) valsuanii* n. sp. A new subjective synonym [*Neobisium (Blothrus) albanorum* Ćurčić, Dimitrijević, Rađa & Vujčić-Karlo, 2006 = *Neobisium (Blothrus) georgecastriotae* Ćurčić, Dimitrijević & Rađa, 2006] is proposed and a key to adults of the *Neobisium (Blothrus)* species from Albania is provided.

Keywords: Taxonomy - new species - new synonymy - Balkans - biospeleology.

INTRODUCTION

The current knowledge about subterranean pseudoscorpions from Albania is very scanty when compared to that of neighbouring Balkan countries. Only three subterranean species of the genus *Neobisium* Chamberlin, 1930, subgenus *Blothrus* Schiödte,1847, are known from southern Albania: *Neobisium (Blothrus) albanicum* (Müller, 1931), *Neobisium (Blothrus) georgecastriotae* Ćurčić, Dimitrijević & Rađa, 2006 in Ćurčić *et al.*, 2006b and *Neobisium (Blothrus) albanorum* Ćurčić, Dimitrijević, Rađa & Vujčić-Karlo, 2006 (see Harvey, 2013). Intensive speleological investigations in Albania carried out from 1990 up till now by F. Didonna and S. Meggiorini (Gruppo Puglia Grotte, Castellana, Bari), A. Gobetti and A. Valsuani (Gruppo Speleologico Piemontese CAI-UGET, Torino) and L. Latella (Museo civico di Storia naturale, Verona) added to our knowledge also about the northern Dinaric karst of this country.

MATERIAL AND METHODS

The specimens were cleared in 5% KOH solution at 30°C for a few hours, washed in distilled water and temporarily mounted, after dissection of palp, chelicera, legs I and IV, in a slide with a well filled with 60% lactic acid. After study each specimen was rinsed in distilled water and returned to a vial with 70% ethanol together with the dissected body parts in glass capillary tubes. All specimens were studied using an Olympus BHB compound microscope; drawings were made with the aid of a Nachet drawing tube. Measurements are given in mm and proportions are given as length/breadth for carapace, chelicerae and pedipalps and as length/depth for legs. Terminology and reference points for measurements largely follow Chamberlin (1931), the relative position of trichobothria along the chelal axis is calculated following Gabbutt (1965), and the use of the terms rallum, antiaxial and paraxial follows Judson (2007).

Holotypes of the new species are deposited in the Muséum d'histoire naturelle, Geneva (Switzerland) and in the Museo civico di Storia naturale, Verona (Italy). Paratypes and other specimens are in the author's collection (Genoa, Italy).

Acronyms: CGG (Collection of Giulio Gardini), MCST (Museo civico di Storia naturale, Trieste), MHNG (Muséum d'histoire naturelle, Geneva), MSNV (Museo civico di Storia naturale, Verona).

The arrangement of species is in alphabetic order.

TAXONOMY

Neobisium (Blothrus) georgecastriotae Ćurčić, Dimitrijević & Rađa, 2006

Figs 1-10

Neobisium georgecastriotae Ćurčić, Dimitrijević & Rađa, in Ćurčić *et al.*, 2006b: 101, figs 1-8.

Neobisium albanorum Ćurčić, Dimitrijević, Rađa & Vujčić-Karlo, 2006: 3, figs 1-30. **New synonym**

Material examined: CGG; 1 male; Albania, Gjirokastër County, Tepelenë, Progonat, Shterra ë Cikes (40°13'19"N, 19°51'43"E), 800 m a.s.l.; 3.VIII.1994; F. Didonna leg. – CGG; 1 tritonymph; Progonat, Shpella ë Kasarit (40°12'38"N, 19°57'24"E), 1100 m a.s.l.; 2.VIII.1994; F Didonna leg.

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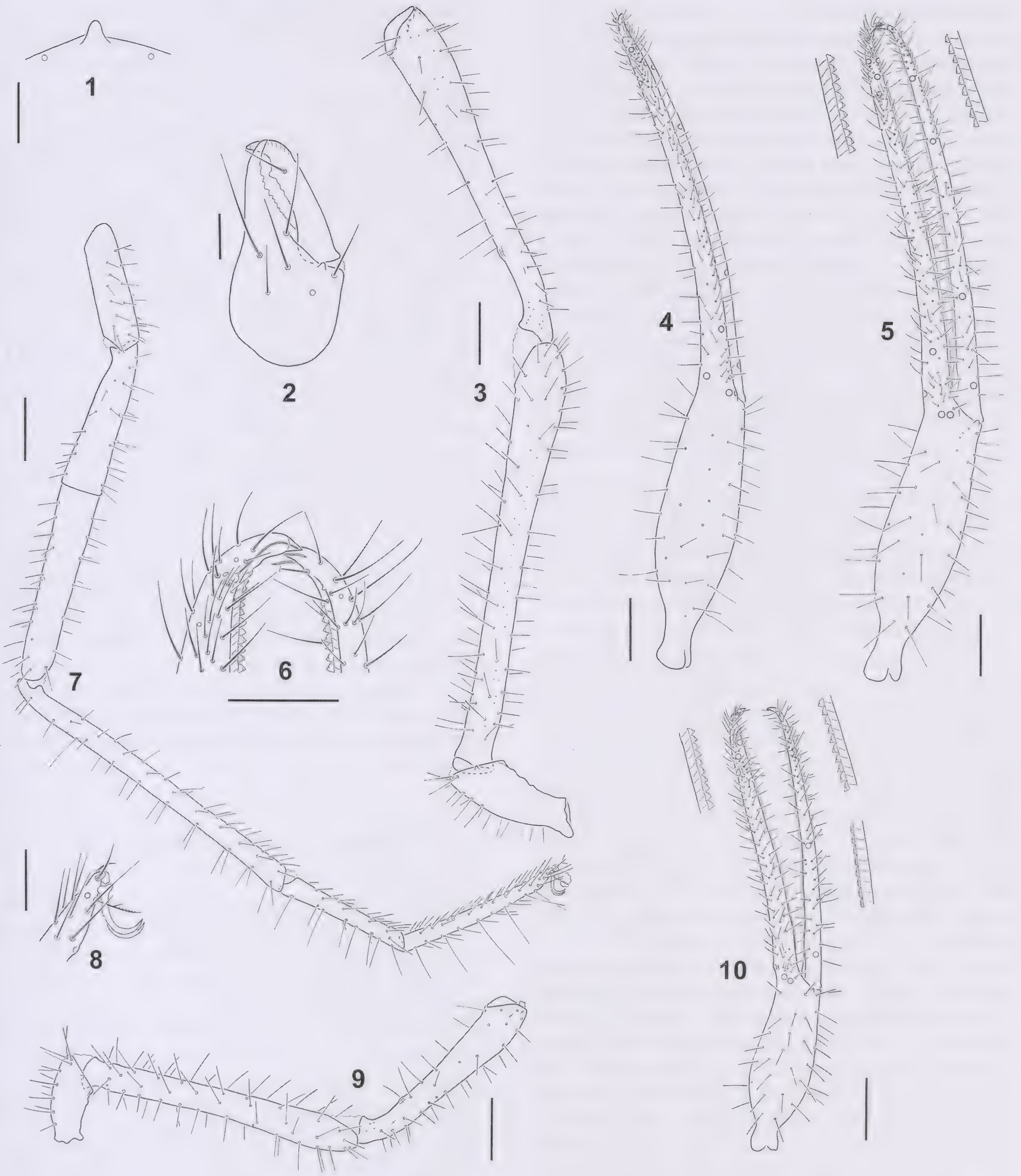
Diagnosis (male, female): A subterranean troglomorphic *Neobisium* that differs from other Balkan species of the genus in the following combination of characters: no eyes or eye-spots; carapace with 4 setae in posterior row, epistome triangular; standard chaetotaxy of tergites I-II 4:4; pedipalps smooth; chelal fingers homodentate, teeth small and contiguous; pedipalpal femur slightly longer than movable finger; ratio between movable finger and hand of chela with pedicel 1.42-1.54; ratio between club and pedicel of patella 2.4-2.6; chela with pedicel length 5.20-5.80 mm, 7.8-8.5 times as long as broad; trichobothrium *ist* just proximal to *est*, the latter midway between *ist-it* or closer to *it*; trichobothrium *et* at level of *it*; trichobothrium *st* closer to *t* than to *sb*; anterolateral process of coxa I squat, apically obtuse.

Description of adults (male, female): Carapace, chelicera, pedipalps and palpal coxae red-brown; pedipalps smooth, pleural membrane granular. Carapace 1.3-1.4 times as long as broad, without eyes or eye-spots, anterior margin with prominent triangular epistome, apically rounded, rarely acuminate (Fig. 1); 20 macrosetae, anterior and posterior rows each with 4 macrosetae, besides 1 or 3 “preocular” setae on each side. Chaetotaxy of tergites I-X 4:4:4-6:4-6:6:6-7:6-7:7-8:7-8:7-8; II and V rarely with 5 setae. Chaetotaxy of sternites II-X (male): 18-30:38-47(15-20 of them situated along posterior margin of genital opening):20-21:15-16:14-15:15-17:14-17:15-16:11-13, setae of genital atrium and median genital sac not seen; chaetotaxy of sternites II-X (female) 12-21:29-31:16-18:13-16:11-15:11-14:12-14:13-14:12-13; sternites III and IV (male, female) each with 2-4 (mostly 3) microsetae in front of each stigma; anal cone with 2 + 2 setae. Chelicera (Fig. 2) 2.0-2.15 (male, female) times as long as broad, palm with 6 setae; fixed finger with 12 subequal teeth proximally decreasing in size; movable finger with a prominent tooth at level of *gs*; *gs* ratio 0.70, spinneret absent or slightly prominent, with 7 silk ducts; rallum with 7-8 blades, the two distal ones dentate; serrulae interior and exterior with 35 and 38 blades, respectively. Manducatory process with 5 setae. Coxal setae: pedipalp 11, I 10, II 9, III 8, IV 13-14; anterolateral process of coxa I squat, apically obtuse. Pedipalp (Figs 3-6): trochanter 2.85 (male) times as long as broad, with a weak button-like tubercle on antiaxial face; femur 8.45-9.0 (male) or 7.7-9.3 (female) times as long as broad, smooth, weakly enlarged distally; patella 6.5-6.9 (male) or 6.6-8.1 (female) times as long as broad, club-shaped, ratio between club and pedicel 2.2-2.5 (male) or 2.6 (female); chela with pedicel 7.8-8.5 (male) or 7.8-7.85 (female) times as long as broad; hand of chela with pedicel 3.2-3.5 (male) or 3.1-3.17 (female) times as long as broad, oval, gradually narrowing towards pedicel; fixed chelal finger with 158-171 (male, female) small contiguous teeth with dental canals (Figs 5-6), venom duct short, nodus ramosus subterminal (Fig. 6); movable chelal finger with 130-138 (male, female) small contiguous teeth with dental canals (Figs 5-6) reaching back near *b*; trichobothria as in Figs 4-5, *ist* just proximal to *est*, the latter midway between *it* and *ist* or closer to *it*; *st* closer to *t* than *sb*; relative position of trichobothria along chelal axis (male from Shterra ë Cikes): *it* 0.085/*et* 0.09/*est* 0.125/*ist* 0.17/*isb* 0.80/*ib* 0.91/*esb* 0.97/*eb* 0.975/*t* 0.15/*st* 0.30/*sb* 0.68/*b* 0.90; ratio between movable finger and hand of chela with pedicel 1.42-1.52 (male) or 1.47-1.54 (female); ratio between pedipalpal femur and movable finger 1.01-1.05 (male, female); ratio between pedipalpal femur and carapace 2.1-2.3 (male, female). Leg I (male from Shterra ë Cikes): trochanter 1.6 times as long as deep, femur 8.5 times as long as deep and 1.5 times longer than patella, the latter 6.3 times as long as deep, tibia 9.9 times, basitarsus 7.2, telotarsus 9.3 times as long as deep, ratio between basitarsus and telotarsus 0.88, subterminal seta dentate, claws with small dorsal tooth; leg IV (male, female) (Figs 7-8): trochanter 3.1-3.55 times as long as deep, femur + patella 7.7-8.25 times as long as deep, tibia 12.1-13.95 times, basitarsus 6.7-7.05 times, telotarsus 9.3-11.6 as long as deep, ratio between basitarsus and telotarsus 0.75-0.82, subterminal seta dentate, claws with small dorsal tooth (Fig. 8).

Measurements: Body length 4.3-5.9 (male, female). Carapace 1.47-1.54 × 0.98-1.13 (male) or 1.51-1.59 × 1.06-1.22 (female). Chelicera 0.94-0.99 × 0.44-0.49 (male) or 1.0-1.02 × 0.48-0.51 (female); movable finger length 0.59-0.64 (male) or 0.65-0.66 (female). Pedipalp: trochanter length 1.06-1.13 (male) or 1.08-1.13 (female); femur 3.23-3.45 × 0.36-0.40 (male) or 3.43-3.54 × 0.37-0.46 (female); patella 2.66-3.02 × 0.41-0.44 (male) or 2.77-3.48 × 0.42-0.43 (female); chela with pedicel 5.20-5.66 × 0.61-0.72 (male) or 5.36-5.80 × 0.68-0.74 (female); hand with pedicel length 2.06-2.32 (male) or 2.11-2.35 (female); movable finger length 3.14-3.38 (male) or 3.25-3.45 (female). Leg I (male from Shterra ë Cikes): trochanter 1.05 x 0.30; femur 1.28 × 0.35; patella 1.59 × 0.325; tibia 2.72 × 0.20; basitarsus 1.15 × 0.17; telotarsus 1.40 × 0.13. Leg IV: trochanter 1.01-1.05 x 0.29-0.33 (male) or 1.01-1.06 x 0.285-0.315 (female); femur + patella 2.84-2.97 × 0.35-0.37 (male) or 2.86-2.91 × 0.37-0.38 (female); tibia 2.66-2.83 × 0.20-0.22 (male) or 2.71-2.76 × 0.21-0.22 (female); basitarsus 1.13-1.16 × 0.16-0.17 (male) or 1.10-1.14 × 0.16-0.17 (female); telotarsus 1.40-1.51 × 0.13-0.15 (male) or 1.40-1.52 × 0.14-0.15 (female).

Short description of tritonymph: Carapace 1.3 times as long as broad, without eyes or eye-spots, anterior margin with a triangular epistome; anterior row with 4, posterior row with 4 (5) setae. Chaetotaxy of tergites I-X 4:4 or 5:4:4 or 7:6 or 7:6:6:6:6 or 7:7. Chelicera 1.9 times as long as broad, palm with 6 setae, fixed finger with subequal teeth, movable



Figs 1-10. *Neobisium (Blothrus) georgecastriotae* Ćurčić, Dimitrijević & Rađa, 2006, male from Shterra ë Cikes (unless otherwise stated). (1) Epistome of carapace. (2) Right chelicera, dorsal view. (3) Trochanter, femur and patella of right pedipalp, dorsal view. (4) Right pedipalpal chela, dorsal view. (5) Same (teeth omitted), antiaxial view, with details of teeth. (6) Apex of chelal fingers, antiaxial view. (7) Right leg IV, antiaxial view. (8) Apex of telotarsus of leg IV, antiaxial view. (9) Tritonymph from Shpella ë Kasarit: trochanter, femur and patella of right pedipalp, dorsal view. (10) Same, right pedipalpal chela (teeth omitted), antiaxial view, with details of teeth. Scale lines: 0.2 mm (1-2, 6, 8); 0.5 mm (3-5, 7, 9-10).

finger with a prominent tooth in distal third; spinneret largely rounded, weakly prominent, with 6-7 silk ducts. Anterolateral process of coxa I squat, apically obtuse. Pedipalp (Figs 9-10): femur 7.9-8.2 times as long as broad, weakly enlarged distally; patella 5.4-5.7 times as long as broad, weakly and gradually enlarged distally, club 2.5 times longer than pedicel; chela with pedicel 7.05-7.3 times as long as broad; hand of chela with pedicel 2.7-2.8 times as long as broad; fixed and movable chelal fingers homodentate, with 118-121 and 98 small and contiguous teeth with dental canals, respectively; trichobothria as in Figs 9-10; relative position of trichobothria along chelal axis (tritonymph from Shterra ë Cikes): *it* 0.10/*et* 0.11/*est* 0.16/*ist* 0.24/ *ib* 0.90/*esb* 0.94/*eb* 0.96/*t* 0.17/*st* 0.50/*b* 0.88; ratio between movable finger and hand of chela with pedicel 1.6; ratio between pedipalpal femur and movable finger 0.98-0.99; ratio between pedipalpal femur and carapace 1.9-2.1.

Measurements: Body length 3.6-4.3. Carapace 1.05-1.19 x 0.80-0.94. Chelicera 0.72-0.75 x 0.38-0.39, movable finger length 0.46-0.49. Pedipalp: femur 2.21-2.33 x 0.28-0.285; patella 1.71 x 0.30-0.315; chela with pedicel 3.66-3.81 x 0.50-0.54; hand with pedicel length 1.40-1.47; movable finger length 2.24-2.34.

Remarks: *Neobisium georgecastriotae* was described on the basis of a single male from the cave Pusi I Kerpajt Pit near Progonat, Gjirokastër County (southern Albania). The species was compared to *N. albanicum* (Müller, 1931), redescribed from a female topotype from the cave Vrima e Dragoit near Paftal, Berat (Beier, 1939, reproduced in Beier, 1963).

Soon afterwards, *N. albanorum* was described on the basis of two males, two females and a tritonymph from two caves near Gjirokastër and Kurvelesh, Gjirokastër County. That nominal species was also compared again to *N. albanicum* and to *N. georgecastriotae*.

However, the diagnostic differences between *N. albanorum* with *N. georgecastriotae* mentioned by Ćurčić and co-workers are based on errors or on a tenuous evaluation of characters: chaetotaxy of tergites I-II is 4:4 in both species (not 6:6 as given for *N. georgecastriotae*), and the proposed differences in size and ratios between the two nominal species (carapace breadth, male pedipalpal length and pedipalpal femur and chela length to breadth ratio, total length of leg IV, femur + patella of leg IV length to breadth ratio) are insubstantial in the light of a well-known high variability in subterranean populations of pseudoscorpions.

In spite of the fact that type specimens of *N. albanorum* and *N. georgecastriotae* (repeatedly requested by e-mail from the Institute of Zoology, University of Belgrade) seem to be currently unavailable for study, a careful comparison of descriptions, measurements and figures from the literature, together with the observation of the close proximity of both type localities (about 20 km apart) and the examination of the male and tritonymph from Progonat, allow the following synonymy to be proposed: *Neobisium albanorum* is a junior subjective synonym of *Neobisium georgecastriotae.* The name "*georgecastriotae*" was published earlier in 2006 and therefore has priority.

Neobisium georgecastriotae is probably closely related to *N. albanicum*. Two syntypes (sex not stated) of *N. albanicum*, glued to card mounts, are stored in the Museo civico di Storia naturale, Trieste. They are labelled: "*Obis. (Blothrus) / albanicum* m. / det. J. Müller" "Vrima e Dragoi / Paftali, Berat / Ravasini 7.22" and "*Blothrus / albanicus* m. / det. J. Müller" "Cotypus" "Vrima e Dragoi / Paftali, Berat / Ravasini 7.22". Thanks to the courtesy of Dr A. Colla (MCST) and F. Gasparo (Trieste), I acquired photographs, basic measurements of pedipalps and position of trichobothria which supplement the description of *N. albanicum* by Beier (1939, 1963). *Neobisium georgecastriotae* differs from *N. albanicum* in size (pedipalpal femur 3.23-3.54 mm vs. 2.74-2.87 mm; patella 2.66-3.48 mm vs. 2.25-2.32 mm; chela 5.20-5.80 mm vs. 4.40-4.55 mm), in ratio between finger and hand of chela (1.42-1.54 vs. 1.62-1.73), in chaetotaxy of tergites I-II (4:4 vs. 6:6) and in position of pedipalpal trichobothria (*ist* slightly proximal to *est* vs. *ist* slightly proximal to *st*; *et* at level or closer to *it* than to *est* vs. *et* halfway between *est* and *it*).

The above redescription of *N. georgecastriotae* incorporates data (chaetotaxy and measurements) from the original description and data proposed by Ćurčić *et al.* (2006c).

Neobisium (Blothrus) latellai n. sp.

Figs 11-18

Holotype: MSNV; female; Albania, Kukes County, Tropoië Municipality, Valbonë, slope S Mt Mali i Thatë, Shpella ë Haxhise (42°28'N, 19°51'E), 1720 m a.s.l.; 8.VII.1993; A. Gobetti & L. Latella leg.

Paratypes: CGG; 2 males 5 females; same data as for holotype.

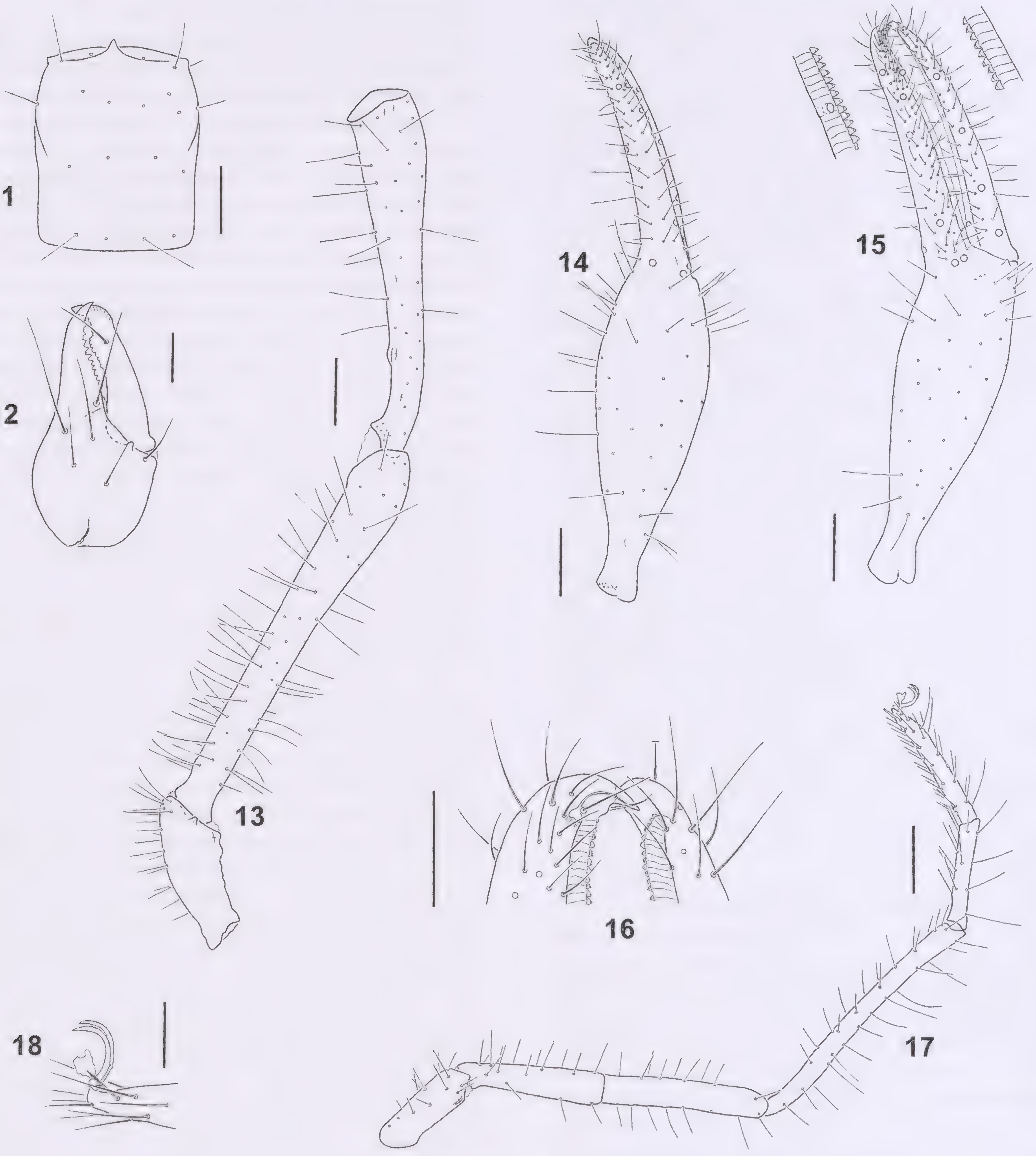
Diagnosis (male, female): A subterranean troglomorphic *Neobisium* that differs from other Dinaric species of the genus in the following combination of characters: no eyes or eye-spots; carapace with 4 setae in posterior row, epistome triangular; standard chaetotaxy of tergites I-II 4:6; pedipalps smooth; chelal fingers homodentate, teeth small and contiguous; pedipalpal femur and hand of chela with pedicel each longer than movable finger; ratio between club and pedicel of patella 2.55-3.0 (male, female); chela with pedicel length 3.95-4.30 mm, and 5.35-5.9 (male, female) times as long as broad; trichobothrium *ist* slightly distal to middle of fixed finger; trichobothrium *st* mostly halfway between *t* and *sb*; anterolateral process of coxa I squat, apically obtuse.

Etymology: Named in honour of Dr Leonardo Latella, entomologist and biospeleologist of the Museo civico di Storia naturale, Verona.

Description of adults (male, female): Carapace, chelicera, pedipalps and palpal coxae red-brown; pedipalps smooth, pleural membrane granular. Carapace (Fig. 11) 1.2-1.4 times as long as broad, without eyes or eye-spots, anterior margin with prominent triangular epistome; 19-21 macrosetae, 4 in anterior and 4 in posterior row, 1 or no "preocular" seta on each side. Chaetotaxy of tergites I-XI 4:6:6:5-7:7:7:7:7-10:8-10:7-10:6-8; tergite I of a male and a female with 5, II-III of two females with 4 setae. Chaetotaxy of sternites II-XI (male): 16-20:37-40(12-14 of them along posterior margin of genital opening): 18-19:15:14:12:13:14:11:10; genital chamber with 2(3) + 2 setae, median sac short and wide; chaetotaxy of sternites II-XI (female) 12-14:26-35:17-18:13-17:13-14:12-14:12-14:12-14:10-14:8-10; sternites III and IV (male, female) with 3 (rarely 2) and 2 (rarely 3) microsetae, respectively, in front of each stigma; anal cone with 2 + 2 setae. Chelicera (Fig. 12) 1.95-2.05 (male, female) times as long as broad, palm with 6 setae; fixed finger with 10-12 subequal teeth proximally decreasing in size; movable finger with 9-12 teeth, 5-6 of them prominent and together at level of *gs*; *gs* ratio 0.68-0.71, spinneret absent or slightly prominent, with 6-8 silk ducts; rallum with 8 blades, the two distal ones dentate; serrulae interior and exterior with 25 and 34-35 blades, respectively. Manducatory process with 5 setae. Coxal setae: pedipalp 8 (rarely 9 or 10), I 6 (rarely 5 or 7), II 6-9, III 6, IV 10-13; anterolateral process of coxa I squat, apically obtuse. Pedipalp (Figs 13-16): trochanter 2.5-2.7 (male, female) times as long as broad, with three or four weak button-like tubercles on antiaxial face; femur 7.27-8.2 (male) or 6.7-7.2 (female) times as long as broad, smooth, weakly and gradually enlarged distally; patella 5.65-5.9 (male) or 5.15-5.5 (female) times as long as broad, club-shaped, ratio between club and pedicel 2.85-3.0 (male) or 2.55-2.7 (female); chela with pedicel 5.45-5.9 (male) or 5.35-5.5 (female) times as long as broad; hand of chela with pedicel 2.95-3.35 (male) or 3.1-3.15 (female) times as long as broad, elongate oval, gradually narrowing towards pedicel; fixed chelal finger with 98-105 (male, female) small contiguous teeth with dental canals (Figs 15-16), venom duct short, nodus ramosus subterminal (Fig. 16); movable chelal finger with 96-103 (male, female) small contiguous teeth with dental canals (Figs 15-16) reaching back beyond *sb*; trichobothria as in Figs 14-15, *ist* slightly distal to middle of fixed finger, *st* mostly halfway between *t* and *sb*; relative position of trichobothria along chelal axis: *it* 0.15-0.17/*et* 0.17-0.19/*est* 0.25-0.28/*ist* 0.40-0.45/*isb* 0.76-0.77/*ib* 0.78-0.85/*esb* 0.91-0.93/*eb* 0.92-0.94/*t* 0.24-0.26/*st* 0.42-0.46/*sb* 0.67-0.70/*b* 0.86-0.88; ratio between movable finger and hand of chela with pedicel 0.85-0.91 (male) or 0.79-0.83 (female); ratio between pedipalpal femur and movable finger 1.52-1.55 (male) or 1.54-1.59 (female); ratio between pedipalpal femur and carapace 2.03-2.10 (male, female). Leg I (male, female): trochanter 1.55-1.65 times as long as deep, femur 6.4-7.3 times as long as deep and 1.4-1.5 times longer than patella, the latter 5.2-6.0 times as long as deep, tibia 6.8-7.8 times, basitarsus 4.25-5.1, telotarsus 5.45-6.8 times as long as deep, ratio between basitarsus and telotarsus 0.75-0.85, subterminal seta dentate, claws with small dorsal tooth; leg IV (male, female) (Figs 17-18): trochanter 2.65-2.95 times as long as deep, femur + patella 9.3-9.8 times as long as deep, ratio between femur and patella 0.75-0.9, tibia 11.3-12.6 times, basitarsus 5.6-6.15 times, telotarsus 7.7-8.15 as long as deep, ratio between basitarsus and telotarsus 0.79-0.82, subterminal seta dentate, claws with small dorsal tooth (Fig. 18).

Measurements: Body length 4.3-4.4 (male) or 5.2-5.7 (female). Carapace 1.43-1.48 × 1.05-1.15 (0.88-0.93 anteriorly) (male) or 1.48-1.55 × 1.24-1.27 (0.96-1.05 anteriorly) (female). Chelicera 0.86 × 0.44 (male) or 0.89-0.96 × 0.455-0.47 (female); movable finger length 0.56-0.63 (male, female). Pedipalp: trochanter 1.03-1.06 × 0.40-0.42 (male) or 1.05-1.20 × 0.41-0.44 (female); femur 2.90-3.11 × 0.38-0.40 (male) or 3.02-3.20 × 0.43-0.46 (female); patella 2.55-2.70 × 0.45-0.46 (male) or 2.57-2.75 × 0.47-0.51 (female); chela with pedicel 3.95-4.04 × 0.67-0.74 (male) or 4.04-4.30 × 0.74-0.80 (female); hand with pedicel length 2.18-2.24 (male) or 2.28-2.54 (female); movable finger length 1.9-2.0 (male) or 1.90-2.02 (female). Leg I: trochanter 0.45 x 0.27 (male) or 0.45-0.50 x 0.29-0.32 (female); femur 1.32 × 0.18 (male) or 1.39-1.43 × 0.20-0.22 (female); patella 0.95 × 0.17 (male) or 0.94-0.98 × 0.16-0.18 (female); tibia 0.92 × 0.135 (male) or 1.0-1.06 × 0.135 (female); basitarsus 0.51 × 0.12 (male) or 0.56-0.59 × 0.11-0.13 (female); telotarsus 0.60 × 0.11 (male) or 0.71-0.75 × 0.11-0.125 (female). Leg IV: trochanter 0.69 x 0.26 (male) or 0.71-0.83 x 0.25-0.28 (female); femur + patella 2.23 × 0.24 (male) or 2.25-2.36 × 0.23-0.25 (female); tibia 1.83 × 0.16 (male) or 1.92-2.02 × 0.16-0.17 (female); basitarsus 0.76 × 0.135 (male) or 0.76-0.85 × 0.125-0.14 (female); telotarsus 0.96 × 0.125 (male) or 0.96-1.04 × 0.12-0.13 (female).

Remarks: Among the subterranean species of *Neobisium*, subgen. *Blothrus*, from the Dinaric Alps, *N. latellai* n. sp. is probably most closely related to *Neobisium (Blothrus) peruni* Ćurčić, 1988 and *Neobisium (Blothrus) perunoides* Ćurčić & Rađa in Ćurčić *et al.*, 2006a, both from caves on Mt Biokovo, Dalmatia, Croatia, with which it shares chiefly the shape of the pedipalpal chela, i.e. with elongate oval hand and short fingers. The main differences among *N. peruni*, *N. perunoides* and *N. latellai* are presented in Table 1.



Figs 11-18. *Neobisium (Blothrus) latellai* n. sp., female holotype. (11) Carapace. (12) Right chelicera, dorsal view. (13) Trochanter, femur and patella of right pedipalp, dorsal view. (14) Right pedipalpal chela, dorsal view. (15) Same (teeth omitted), antiaxial view, with details of teeth. (16) Apex of chelal fingers, antiaxial view. (17) Right leg IV, antiaxial view. (18) Apex of telotarsus of leg IV, antiaxial view. Scale lines: 0.2 mm (12, 16, 18); 0.5 mm (11, 13-15, 17).

***Neobisium (Blothrus) valsuanii* n. sp.**

Figs 19-26

Holotype: MHNG; male; Albania, Dibër County, Mat, Burrel, Macukull, Shpella Haruska (5 km SSE of Valgjini) (41°39'53"N, 20°07'54"E), 1480 m a.s.l.; 28.VI.2015; A. Valsuani leg.

Paratypes: CGG; 1 female; same data as for holotype. – CGG; 1 male; Albania, Dibër County, Mat, Burrel, Macukull, Shpella Bushiti (near Valgjini) (41°25'44"N, 20°03'58"E), 1131 m a.s.l.; IV.2014; A. Valsuani leg. – CGG; 1 female; Albania, Dibër County, Mat, Burrel, Macukull, Shpella Linozi-Leftari, 1868 m a.s.l.; 10.VII.2015; A. Valsuani leg.

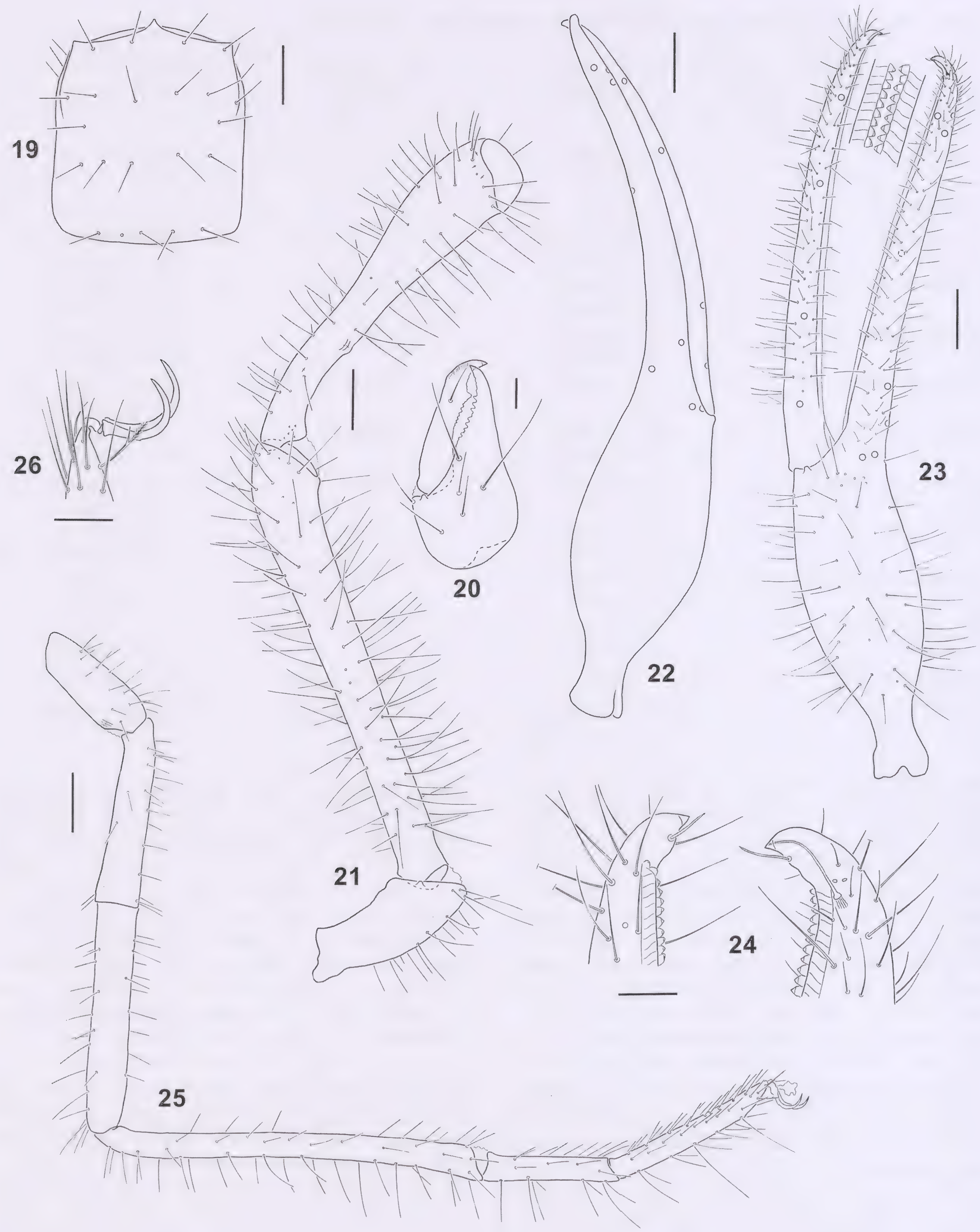
Table 1. Main distinctive characters between *N. peruni*, *N. perunoides* and *N. latellai* n. sp.

	N. peruni (male, female)	*N. perunoides* (female)	*N. latellai* n. sp. (male, female)
Carapace			
Posterior setae	6-7 (male) 4 (female)	6	4 (male, female)
Pedipalp			
Femur length	3.69-3.875 (male) 4.14 (female)	4.14	2.90-3.11 (male) 3.02-3.20 (female)
Patella length	2.95-3.155 (male) 3.46 (female)	3.45	2.55-2.70 (male) 2.57-2.75 (female)
Patella length/breadth ratio	5.12-5.44 (male) 6.47 (female)	5.23	5.66-5.87 (male) 5.14-5.50 (female)
Patella club/pedicel ratio	2.3-2.6 (male)	2.3	2.8-3.0 (male) 2.55-2.7 (female)
Chela length	5.33-5.61 (male) 6.13 (female)	6.08	3.95-4.04 (male) 4.06-4.30 (female)
Chela length/breadth ratio	6.03-6.48 (male) 7.86 (female)	5.02	5.46-5.90 (male) 5.35-5.48 (female)
Finger length	2.76-2.83 (male) 3.66 (female)	2.87	1.90-2.0 (male) 1.90-2.02 (female)
Finger/hand with ped. ratio	1.02-1.07 (male) 1.48 (female)	0.89	0.85-0.91 (male) 0.79-0.83 (female)
Femur/finger ratio	1.33-1.37 (male) 1.13 (female)	1.44	1.52-1.55 (male) 1.54-1.59 (female)
Trichobothrium *ist*	distal to middle of finger	distal to middle of finger	near middle of finger
Trichobothrium *st*	closer to *t* than to *sb*	closer to *t* than to *sb*	halfway between *t* and *sb*

Diagnosis (male, female): A large subterranean troglomorphic *Neobisium* that differs from other Dinaric species of the genus in the following combination of characters: no eyes or eye-spots; carapace with 6 setae in posterior row, epistome triangular; standard chaetotaxy of tergites I-II 6:6; pedipalps smooth; chelal fingers homodentate, teeth small and contiguous; pedipalpal femur slightly longer than movable finger, the latter longer than hand of chela with pedicel; ratio between club and pedicel of patella 1.65-1.95 (male, female); chela with pedicel length 5.8-6.35 mm, 4.75-5.6 (male, female) times as long as broad; trichobothrium *ist* near middle of fixed finger; trichobothrium *st* closer to *t* than to *sb*; anterolateral process of coxa I squat, apically obtuse.

Etymology: Named in honour of Alessandro Valsuani, who first collected the species during speleological research in Albania coordinated by A. Gobetti (Gruppo Speleologico Piemontese CAI-UGET, Torino).

Description of adults (male, female): Carapace, chelicera, pedipalps and palpal coxae red-brown; pedipalps smooth, pleural membrane granular. Carapace (Fig. 19) 1.1-1.2 times as long as broad, without eyes or eye-spots, anterior margin with prominent triangular epistome, apically rounded, rarely acuminate; 22-24 macrosetae, 4 in anterior and (5)6 in posterior row, besides 2 or 3 "preocular" setae on each side. Chaetotaxy of tergites I-XI 5-7:6-7:6-7:6-8:7-10:7-10:8-10:9-11:10-11:8-11:10; tergite I of a male and a female with 6, of a male with 5, of a female with 7 setae; sternite II of a female with 7 setae. Chaetotaxy of sternites II-XI (male): 26-29:52-53(29-30 of them along posterior margin of genital opening):19-20:15-20:18:17-18:18:17-18:17:13, setae of genital atrium and median genital sac not seen; chaetotaxy of sternites II-XI (female) 12:24-27:20-22:17-18:17-20:16-22:16-20:17-21:16-20:14-16; sternites III and IV (male, female) with 4-5 (rarely 3 or 6) and 4-5 (rarely 3) microsetae in front of each stigma, respectively; anal cone with 2 + 2 setae. Chelicera (Fig. 20) 1.95-2.1 (male, female) times as long as broad, palm with 6 (rarely 7) setae; fixed finger with 11-13 subequal teeth proximally decreasing in size; movable finger with 7-11 teeth, most of them prominent and situated together at level of *gs*; *gs* ratio 0.68-0.71, spinneret absent or slightly prominent, with 10-12 silk ducts; rallum with 13-17 blades, the two distal ones dentate; serrulae interior and exterior with 37-40 and 40-42 blades, respectively. Manducatory process with 5-7 (mostly 5) setae. Coxal setae: pedipalp 9-12 (mostly 9), I 5-9 (mostly 8), II 6-10, III 7-9 (mostly 8),



Figs 19-26. *Neobisium (Blothrus) valsuanii* n. sp., male holotype (unless otherwise stated). (19) Carapace. (20) Left chelicera, dorsal view. (21) Trochanter, femur and patella of left pedipalp, dorsal view. (22) male paratype from Shpella Bushiti: right pedipalpal chela (setae omitted), dorsal view. (23) Left pedipalpal chela (teeth omitted), paraxial view, with details of teeth. (24) Apex of chelal fingers, paraxial view. (25) Right leg IV, paraxial view. (26) Apex of telotarsus of leg IV, paraxial view. Scale lines: 0.2 mm (20, 24, 26); 0.5 mm (19, 21-23, 25).

IV 14-19 (mostly 19); anterolateral process of coxa I squat, apically obtuse. Pedipalp (Figs 21-24): trochanter 2.4-2.6 (male, female) times as long as broad, with a weak button-like tubercle on antiaxial face; femur 6.5-6.8 (male) or 6.15-6.5 (female) times as long as broad, smooth, weakly enlarged distally; patella 4.3-5.0 (male) or 4.45-4.5 (female) times as long as broad, club-shaped, ratio between club and pedicel 1.7-1.85 (male) or 1.65-1.95 (female); chela with pedicel 5.25-5.6 (male) or 4.7-4.75 (female) times as long as broad; hand of chela with pedicel 2.45-2.6 (male) or 2.25-2.4 (female) times as long as broad, oval, abruptly narrowed towards pedicel; fixed chelal finger with 120-140 (male, female) small contiguous teeth with dental canals (Figs 23-24), venom duct short, nodus ramosus subterminal (Fig. 24); movable chelal finger with 118-140 (male, female) small contiguous teeth with dental canals (Figs 23-24) reaching back near *b*; trichobothria as in Figs 22-23, *ist* near middle of fixed finger, *st* closer to *t* than to *sb*; relative position of trichobothria along chelal axis: *it* 0.125-0.145/*et* 0.14-0.155/*est* 0.17-0.19/*ist* 0.45-0.50/*isb* 0.75-0.85/*ib* 0.85-0.90/*esb* 0.90-1.0/*eb* 0.95-1.0/*t* 0.15-0.19/*st* 0.325-0.395/*sb* 0.68-0.79/*b* 0.88-0.935; ratio between movable finger and hand of chela with pedicel 1.26-1.32 (male) or 1.11-1.26 (female); ratio between pedipalpal femur and movable finger 1.08 (male) or 1.11-1.12 (female); ratio between pedipalpal femur and carapace 1.85-2.15 (male, female). Leg I (male, female): trochanter 1.48-1.55 times as long as deep, femur 5.9-6.4 times as long as deep and 1.4-1.5 times longer than patella, the latter 4.35-4.8 times as long as deep, tibia 6.8-7.85 times, basitarsus 4.75-5.2, telotarsus 6.2-6.8 times as long as deep, ratio between basitarsus and telotarsus 0.75-0.83, subterminal seta dentate, claws with small dorsal tooth; leg IV (male, female) (Figs 25-26): trochanter 2.7-3.1 times as long as deep, femur + patella 8.0-9.7 times as long as deep, ratio between femur and patella 0.79-0.83, tibia 12.5-13.0 times, basitarsus 5.0-5.6 times, telotarsus 7.05-8.45 as long as deep, ratio between basitarsus and telotarsus 0.73-0.77, subterminal seta dentate, claws with small dorsal tooth (Fig. 26).

Measurements: Body length 6.7 (male) or 7.3-8.1 (female). Carapace 1.87-1.98 × 1.60-1.61 (1.37-1.41 anteriorly) (male) or 1.96-1.98 × 1.70-1.79 (1.47-1.57 anteriorly) (female). Chelicera 1.36-1.48 × 0.70-0.705 (male) or 1.43-1.60 × 0.69-0.81 (female); movable finger length 0.92-1.0 (male) or 0.96-1.1 (female). Pedipalp: trochanter 1.50 × 0.58-0.59 (male) or 1.53-1.58 × 0.61-0.65 (female); femur 3.70-4.01 × 0.57-0.59 (male) or 3.90-3.99 × 0.60-0.65 (female); patella 2.90-3.22 × 0.64-0.67 (male) or 3.10-3.35 × 0.69-0.75 (female); chela with pedicel 5.8-6.0 × 1.07-1.10 (male) or 5.83-6.35 × 1.23-1.33 (female); hand with pedicel length 2.7-2.8 (male) or 2.78-3.20 (female); movable finger length 3.41-3.70 (male) or 3.50-3.55 (female). Leg I: trochanter 0.61-0.66 x 0.41-0.43 (male) or 0.62 x 0.40 (female); femur 1.98-2.06 × 0.31-0.34 (male) or 1.90 × 0.32 (female); patella 1.39 × 0.29-0.32 (male) or 1.38 × 0.31 (female); tibia 1.57-1.59 × 0.20-0.23 (male) or 1.56 × 0.23 (female); basitarsus 0.87-0.94 × 0.17-0.18 (male) or 0.86 × 0.18 (female); telotarsus 1.13-1.16 × 0.17-0.18 (male) or 1.12 × 0.18 (female). Leg IV: trochanter 1.05-1.12 x 0.36-0.39 (male) or 1.07 x 0.38 (female); femur + patella 3.40-3.49 × 0.36-0.38 (male) or 3.22 × 0.40 (female); tibia 3.25-3.39 × 0.25-0.27 (male) or 3.11 × 0.30 (female); basitarsus 1.12-1.15 × 0.20-0.23 (male) or 1.09 × 0.22 (female); telotarsus 1.48-1.52 × 0.18-0.21 (male) or 1.36 × 0.21 (female).

Remarks: Among the subterranean species of *Neobisium*, subgen. *Blothrus*, from the Dinaric Alps, *N. valsuanii* n. sp. is probably most closely related to *Neobisium (Blothrus) carnae carnae* Beier, 1938, *Neobisium (Blothrus) carnae fraternum* Beier, 1939 and *Neobisium (Blothrus) anaisae* Ćurčić & Lemaire in Ćurčić *et al.*, 2009, the two former species from caves of Radoš Planina (Bosnia-Herzegovina), the latter from Krapa (Macedonia). The main differences between these species and subspecies are presented in Table 2.

Neobisium (Blothrus) cf. *vjetrenicae* Hadži, 1932
Figs 27-29

Neobisium (Blothrus) vjetrenicae Hadži, 1932: 102, figs 1-4. – Hadži, 1933: 49, figs 1-2. – Beier, 1939: 70, figs 84-85. – Beier, 1963: 151, fig. 155.

Material examined: CGG; 1 ♂; Albania, Shkodër County, Shkodër, Bogë, Dotek Pass, Helmit Abyss, 1540 m a.s.l.; VIII.1995; S. Meggiorini leg.

Short description of adult (male): Carapace, chelicera, pedipalps and palpal coxae red-brown; pedipalps smooth, pleural membrane granular. Carapace 1.2 times as long as broad, without eyes or eye-spots, anterior margin with a triangular epistome; anterior row with 4, posterior row with 5 setae. Chaetotaxy of tergites I-XI 4:4:6:7:7:7:8:9:8:9:6. Chaetotaxy of sternites III-X: (4)28(3):(3)14(3):17:16:17:16:14:8. Chelicera 2.0 times as long as broad, palm with 6 setae, fixed finger with 10 subequal teeth, movable finger with a prominent tooth in the distal third; spinneret largely rounded, weakly prominent. Anterolateral process of coxa I squat, apically obtuse. Pedipalp (Figs 27-29): trochanter 2.6 times as long as broad, with one weak button-like tubercle on antiaxial face; femur 7.6 times as long as broad, weakly enlarged distally; patella 5.3 times as long as broad, weakly and gradually enlarged distally, club 2.54 times longer than pedicel; chela with pedicel 6.3 times as long as broad; hand of chela with pedicel 3.0 times as long as broad; fixed and movable chelal fingers homodentate, with 110 and 109 small and contiguous teeth with dental canals, respectively; trichobothria as in Figs 28-29; relative position of

Table 2. Main distinctive characters between *N. c. carnae*, *N. c. fraternum*, *N. anaisae* and *N. valsuanii* n. sp.

	N. c. carnae (female)	*N. c. fraternum* (female)	*N. anaisae* (female)	*N. valsuanii* n. sp. (male, female)
Carapace				
Posterior setae	6	6	4	6
Tergites				
Setae of tergites I-II	4:6	6:8	4:4	6:6
Chelicera				
Blades of rallum	-	-	8-9	13-17
Pedipalp				
Femur length	3.25	2.98	3.88	3.70-4.01
Femur length/breadth ratio	7.1	6.8	8.4	6.5-6.8 (male) 6.15-6.5 (female)
Patella length	2.70	2.50	3.30	2.90-3.35
Patella length/breadth ratio	5.0	4.7	6.1	4.33-5.03 (male) 4.46-4.49 (female)
Patella club/pedicel ratio	2.8	2.7	2.5	1.65-1.95
Chela with pedicel length	5.2	4.62	5.53	5.8-6.35
Chela length/breadth ratio	5.6	4.9	5.75	5.27-5.6 (male) 4.74-4.77 (female)
Finger length	2.75	2.42	3.17	3.4-3.7
Teeth on fixed/movable finger	-	-	159/121	120-140/118-140
Finger/hand with ped. ratio	1.06	1.03	1.34	1.26-1.32 (male) 1.11-1.26 (female)
Femur/finger ratio	1.18	1.23	1.22	1.08-1.12
Trichobothrium *ist*	distal to middle of finger	distal to middle of finger	near middle of finger	near middle of finger

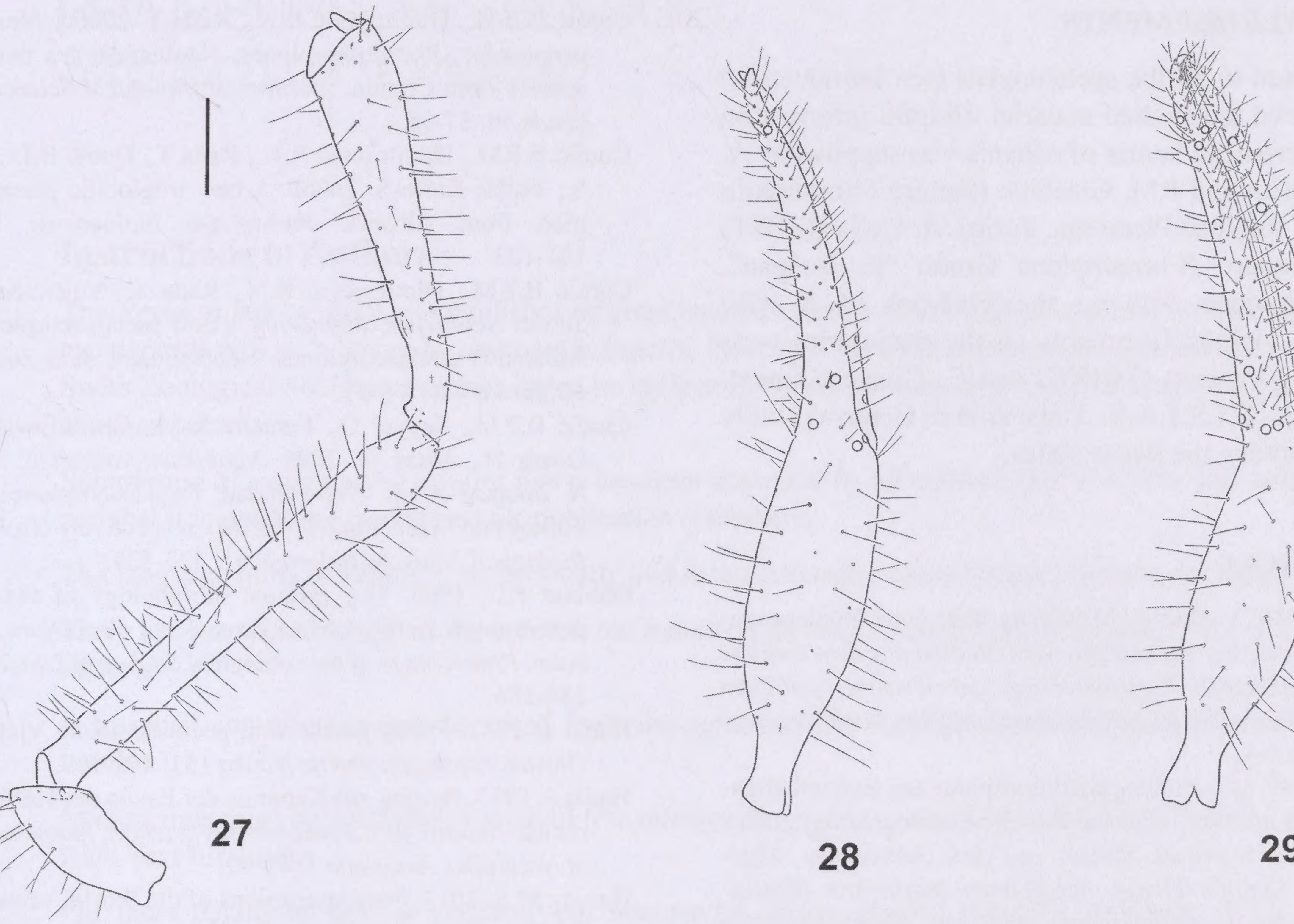
trichobothria along chelal axis: *it* 0.14/*et* 0.18/*est* 0.22/*ist* 0.40/*isb* 0.76/*ib* 0.87/*esb* 0.90/*eb* 0.91/*t* 0.235/*st* 0.41/*sb* 0.725/*b* 0.88; ratio between movable finger and hand of chela with pedicel 1.16; ratio between pedipalpal femur and movable finger 1.30; ratio between pedipalpal femur and carapace 2.10.

Measurements: Body length 5.3. Carapace 1.34 x 1.12 (0.91 anteriorly). Chelicera 0.88 x 0.44, movable finger length 0.57. Pedipalp: trochanter 0.99 x 0.38; femur 2.82 x 0.37; patella 2.28 x 0.43; chela with pedicel 3.90 x 0.62; hand with pedicel length 1.86; movable finger length 2.16.

Remarks: *Neobisium vjetrenicae* was described by Hadži (1932, German translation in Hadži, 1933) on the basis of a single male collected in the cave Pećina Vjetrenica (42°50’45”N, 17°59’02”E) near Zavala, Bosnia and Herzegovina. The species was subsequently redescribed by Beier (1939, reproduced in Beier, 1963) from topotypical specimens of both sexes.

The male from the Helmit Abyss, Albania, is here provisionally asigned to *N. vjetrenicae*, with which it shares the following characters: epistome triangular, posterior margin of carapace with 4 setae; tergites I-II with 4 setae; pedipalps smooth; chelal fingers homodentate, teeth small and contiguous; pedipalpal femur longer than movable finger, and movable finger longer than hand of chela with pedicel; chela with pedicel 6.3 times as long as broad; trichobothrium *ist* slightly distal to middle of fixed finger; trichobothrium *st* closer to *t* than to *sb*; anterolateral process of coxa I squat, apically obtuse.

Size and ratios of pedipalpal segments are similar in males from both caves: Vjetrenica - femur length 2.30-2.32 (x7.4), patella 1.80-1.88 (x5.0), club/pedicel of patella x2.6, chela with pedicel 3.60-3.61 (x6.2), hand with pedicel 1.73 (x3.0), finger 1.90-2.02, finger/hand with pedicel x1.17-1.20, femur/finger x1.15-1.21; Helmit - femur length 2.82 (x7.6), patella 2.28 (x5.3), club/pedicel of patella x2.54, chela with pedicel 3.9 (x6.3), hand with pedicel 1.86 (x3.0), finger 2.16, finger/hand with pedicel 1.16, femur/finger 1.30. In the male from Vjetrenica (Beier, 1939: 70, fig. 84) trichobothrium *ist* of the fixed chelal finger seems to be more distal than in the male from Helmit (Figs 28-29) and the teeth on the chelal fingers are 130 in the male from Vjetrenica (Hadži, 1933) versus 109-110 in the male from Helmit.



Figs 27-29. *Neobisium (Blothrus)* cf. *vjetrenicae* Hadži, 1932, male from Helmit Abyss. (27) Trochanter, femur and patella of right pedipalp, dorsal view. (28) Right pedipalpal chela, dorsal view. (29) Right pedipalpal chela (teeth omitted), paraxial view. Scale line: 0.5 mm.

Key to adults of the *Neobisium (Blothrus)* species from Albania
[*N. (B.)* cf. *vjetrenicae* not included]

1A Tergites I-II with 4:4 or 6:6 setae; ratio between pedipalpal finger and hand of chela with pedicel 1.1-1.7; ratio between pedipalpal femur and finger 0.95-1.3; movable chelal finger with trichobothrium *st* closer to *t* than to *sb* 2

1B Tergites I-II with 4:6 setae; ratio between pedipalpal finger and hand of chela with pedicel 0.8-0.9; ratio between pedipalpal femur and finger 1.5-1.6; movable chelal finger with trichobothrium *st* halfway between *sb* and *t* .... *N. (B.) latellai* n. sp.

2A Carapace with 4 setae in posterior row; pedipalps elongate: patella 5.3-8.1, chela with pedicel 6.3-8.6 times as long as broad; ratio between club and pedicel of patella 2.4-2.6 3

2B Carapace with 6 setae in posterior row; pedipalps thick: patella 4.3-5.0, chela with pedicel 4.7-5.6 times as long as broad; ratio between club and pedicel of patella 1.65-1.95 .... *N. (B.) valsuanii* n. sp.

3A Tergites I-II with 4:4 setae; ratio between pedipalpal finger and hand of chela with pedicel 1.4-1.5; length of pedipalpal chela 5.2-5.8; fixed chelal finger with trichobothrium *ist* just proximal to *est*; trichobothrium *est* midway between *ist-it* or closer to *it*; trichobothrium *et* at level of *it* .... *N. (B.) georgecastriotae*

3B Tergites I-II with 6:6 setae; ratio between pedipalpal finger and hand of chela with pedicel 1.6-1.7; length of pedipalpal chela 4.4-4.55; fixed chelal finger with trichobothrium *ist* just proximal to *st*, trichobothrium *est* closer to *it* than to *ist*; trichobothrium *et* midway between *est-it* .... *N. (B.) albanicum*

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REFERENCES

Beier M. 1938. Vorläufige Mitteilung über neue Höhlenpseudoscorpione der Balkanhalbinsel. *Studien aus dem Gebiete der Allgemeinen Karstforschung, der Wissenschaftlichen Höhlenkunde, der Eiszeitforschung und den Nachbargebieten* 3(8): 5-8.

Beier M. 1939. Die Höhlenpseudoscorpione der Balkanhalbinsel. Eine auf dem Material der „Biospeologica balcanica" basierende Synopsis. *Studien aus dem Gebiete der Allgemeinen Karstforschung, der Wissenschaftlichen Höhlenkunde, der Eiszeitforschung und den Nachbargebieten* 4(10): 1-83.

Beier M. 1963. Ordnung Pseudoscorpionidea (Afterskorpione). Bestimmungsbücher zur Bodenfauna Europas, vol. 1. *Akademie-Verlag, Berlin*, vi + 313 pp.

Chamberlin J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part II. The Diplosphyronida (Arachnida-Chelonethida). *Annals and Magazine of Natural History* (10)5: 1-48, 585-620.

Chamberlin J.C. 1931. The arachnid order Chelonethida. *Stanford University Publications, University Series (Biol. Sci.)* 7: 1-284.

Ćurčić B.P.M. 1988. Cave-dwelling Pseudoscorpions of the Dinaric Karst. *Slovenska Akademija Znanosti in Umetnosti, Ljubljana*, 191 pp.

Ćurčić B.P.M., Dimitrijević R.N., Rađa T. 2006a. *Neobisium perunoides* (Pseudoscorpiones, Neobisiidae), a new cave species from Croatia. *Archives of Biological Sciences Belgrade* 58: 37-38.

Ćurčić B.P.M., Dimitrijević R.N., Rađa T., Dudić B.D., Šimić S., Vujčić-Karlo S. 2006b. A new troglobitic pseudoscorpion from Albania. *Periodicum biologorum* 108(1): 101-103.

Ćurčić B.P.M., Dimitrijević R.N., Rađa T., Vujčić-Karlo S. 2006c. *Neobisium albanorum*, a new pseudoscorpion from Albania (Pseudoscorpiones: Neobisiidae). *Acta Zoologica Bulgarica* 58(1): 3-11.

Ćurčić B.P.M., Sayyar O., Lemaire J.-M., Dimitrijević R.N., Demir H., Aktaş M. 2009. *Neobisium yozgati* n. sp. and *N. anaisae* n. sp. (Neobisiidae, Pseudoscorpiones) from Turkey and Macedonia (FYROM), respectively. *Archives of Biological Sciences Belgrade* 61: 523-529.

Gabbutt P.D. 1965. The external morphology of two pseudoscorpions, *Neobisium carpenteri* and *Neobisium maritimum*. *Proceedings of the zoological Society of London* 145: 359-386.

Hadži J. 1932. Prilog poznavanju pecinske faune Vjetrenice. *Glasnik SrpskeAkademije Nauka* 151: 101-157.

Hadži J. 1933. Beitrag zur Kenntnis der Fauna der Höhle Vjetrenica. *Bulletin de l'Académie des Sciences Mathématiques et Naturelles, Belgrade* 1: 49-79.

Harvey M.S. 2013. Pseudoscorpions of the World, version 3.0. Western Australian Museum, Perth. Available at: http://www.wa.gov.au/catalogues-beta/pseudoscorpions (accessed 30 October 2017).

Judson M.L.I. 2007. A new and endangered species of the pseudoscorpion genus *Lagynochthonius* from a cave in Vietnam, with notes on chelal morphology and the composition of the Tyrannochthoniini (Arachnida, Chelonethi, Chthoniidae). *Zootaxa* 1627: 53-68.

Müller G. 1931. Nuovi pseudoscorpioni cavernicoli appartenenti al sottogenere *Blothrus* Schioedte (diagnosi preliminari). *Bollettino della Società entomologica italiana* 63: 125-127.

Schiödte J.C. 1847. Undersögelser over den underjordiske Fauna i Hulerne i Krain og Istrien. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlingar* 6: 75-81.

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